The Role of Individual Cognitive and Behavioral Ontogeny in Organization and Evolution of Social Systems

Andrew G. Fulmer
The Graduate Center, City University of New York
THE ROLE OF INDIVIDUAL COGNITIVE AND BEHAVIORAL ONTOGENY IN ORGANIZATION AND EVOLUTION OF SOCIAL SYSTEMS

by

ANDREW GOLDKLANK FULMER

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Andrew Goldklank Fulmer

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Date

Mark E. Hauber
Chair of Examination Committee

Date

Richard Bodnar
Acting Executive Officer

Supervisory committee:

Thomas Preuss
Hunter College, CUNY

Dan P. McCloskey
College of Staten Island, CUNY

Janis Dickinson
Cornell University, Lab of Ornithology

THE CITY UNIVERSITY OF NEW YORK
ABSTRACT

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Andrew Goldklank Fulmer

Advisor: Mark E. Hauber

Exploration and explanation of the relationship between individual variation in behavior and the composition and adaptive success of social groups or populations are crucial problems in the fields of behavioral ecology, ethology, and comparative psychology. These questions have been the subject of a longstanding discussion at both the proximate and ultimate levels of inquiry. Adaptive mechanisms explaining social decision making, both in terms of affiliative and competitive partner choices, are at the center of such discussions. Inclusive fitness, kin-selection, handicap or prestige, risk seeking and risk avoiding strategies, pay-to-stay/reward principles, as well as other theories have been proposed and supported as these mechanisms in a variety of taxa; theories which may not be mutually exclusive. This dissertation focuses on the role of individual ontogeny in the organization of a series of charismatic social systems. Specifically, I review evolutionary aspects of siblicidal and brood parasitic systems, and present research on social/cognitive ontogeny and interactive behavior of a passerine avian cooperative breeder (Turdoides squamiceps), a phenotypically reversible teleost fish (Astatotilapia burtoni), and a eusocial mammal (Heterocephalus glaber). The theme adaptive behavioral response to
fluctuating or uncertain environments and interactions unites these taxonomically diverse subjects.

In Chapter 1 I review a potential evolutionary trajectory from siblicidal behavior to both obligate and intraspecific brood parasitism. This analysis focuses on a series of fitness inequalities that may function as the most parsimonious explanation of such an evolutionary trajectory. When resources provided by parents are limited, full siblings may be driven to siblicide. The inherent fitness cost to parents of siblicidal behavior by offspring may be offset by brood parasitism. Brood parasitism, however, carries its own costs, both in conspecific/intraspecific brood parasitism (where individuals in a population may still be related, requiring a kin-selected balance for any fitness advantage to result) and in interspecific brood parasitism, where the host may not be equipped to nourish offspring as effectively as biological parents. Chapter 1 also discusses the ultimate mechanisms for the evolution of one ontogenetic style to the others. For intraspecific brood parasitism to evolve from siblicide, the alleles shared with the parasitic parents by the surviving, parasitically laid offspring must exceed those eliminated from the population via competition between the parasitically laid offspring and host offspring. For interspecific brood parasitism to evolve from siblicide or intraspecific brood parasitism, offspring lost to siblicide or related individuals lost to intraspecific brood parasitism must be less than those lost to nutritional or behavioral mismatches which result from heterospecific parental care by foreign host taxa.

Chapters 2 and 3 were developed in association with the Arabian Babbler Research Project, a 40+ year old ongoing study using a habituated and ID banded population of Arabian Babblers in Hazeva, Israel, maintained by Professor Amotz Zahavi. The habituation of these cooperatively breeding passerines to observer presence permits detailed long-term data sets and
analysis of individual life histories. Arabian Babblers live in exclusive, male philopatric social groups with high reproductive skew, where rank is strongly positively correlated with age. In Chapter 2 I demonstrate the relationship between ontogenetic experience and developmental stage and neophilic behavior in young Arabian Babblers (Turdoides squamiceps). I used a series of novel/familiar stimulus presentations to identify the latency to and frequency of approach to stimuli by young individuals. Stimuli yielded multimodal comparisons, including stationary objects, moving objects, and sounds. Each had a familiar and a novel condition. I found that all birds approached novel stimuli more frequently than they did familiar stimuli, and that intrabrood rank positively predicted frequency of approach. Additionally, juveniles were more likely to approach novel stimuli, and did so earlier in the presentation trials, than fledglings. All young individuals were more likely to approach when adults were present.

In Chapter 3 I use a dataset collected from 2002-2004 by members of the Arabian Babbler Research Project which details the behaviors occurring before and during the formation of allopreening dyads. Chapter 3 analyzes the role of autopreening in the formation of allopreening dyads, and presents evidence that it is a displacement behavior. Autopreening may occur before the social approach that is necessary to form an allopreening dyad. When relationships were hierarchically more certain (represented by an older actor in the dyad, or the formation of the dyad without invitation by the recipient) approach by the recipient occurred without autopreening. When recipients did autopreen, they were significantly less likely to approach the actor to form the dyad.

In Chapter 4 I present data from observation of a phenotypically reversible cichlid fish Astatotilapia burtoni. Socially mediated morphological plasticity in this species is largely driven by male intrasexual competition, and it is physiologically necessary for a male to develop the
territorial phenotype in order to reproduce. Traditionally, analysis of *A. burtoni* communities divides males between territorial (DOM) and non-territorial (SUB) individuals based on an index that subtracts the total losses of an individual in intrasexual conflict from the combined total wins and courtship behavior exhibited by that individual. There are dramatic morphological, physiological, and behavioral differences between these two categories, defined as having either positive (DOM) or negative (SUB) dominance index scores. Chapter 4 uses cluster analyses to propose a formalization of a third male phenotype, identified with individuals transitioning between prototypical DOMs and prototypical SUBs. Specifically, a novel behavior was identified; a potential risk-avoidance strategy in which individuals appear to ignore challenges, rather than engage or flee. Other unique behavioral traits of this male phenotype, such as frequency of certain pigment displays, were identified, and the individuals were shown to be those more likely to transition across the traditional DOM/SUB division point of a zero score on the dominance index than either prototypical DOMs or prototypical SUBs.

In Chapter 5 I present the results of a preliminary rescue-behavior experiment using a eusocial mammal, the Naked Mole-Rat *Heterocephalus glaber*. The study population was individually tracked using subcutaneous RFID tags. This method permits high temporal resolution on location of individuals. The rescue scenario involved the experimental trapping of individuals at the distal end of tubes connected to the central enclosure. Cork was used to create an artificial “cave-in” that served as an obstacle for colony members. A plastic barrier prevented the escape of trapped individuals. A second permutation of the experiment used a bifurcated tube to present experimentally trapped individuals and empty space, both blocked by cork, simultaneously. Colony members were significantly quicker to excavate trapped individuals than empty space. Effort expended (defined as time spent in rescue and latency to initiation of rescue)
varied by both caste and individual, with queens expending less effort than workers, and individuals initiating rescue events also being the most frequent actors in excavation.

In Chapter 6 I discuss the connections among these findings, as well as their relevance to contemporary questions in research on behavioral ecology and comparative psychology. Together, these manuscripts provide a taxonomically varied perspective on a central issue in sociobiology and cognitive ethology: the illumination of the role of individual ontogenetic experience on the adaptive function of social groups. This dissertation does not attempt to represent an exhaustive investigation of this complex subject. Instead, it highlights promising avenues of investigation and demonstrates that social systems which may differ greatly in organization and evolutionary history remain strongly influenced and constructed by interindividual variation in ontogeny and experience, with particular regard to decision making.
This dissertation is dedicated to Kanji, Nugget, and Hearth, my first and primary interspecific interactions.

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proposal, improving not only the scope and structure of the questions being asked, but also the relevance to the larger study of cooperatively breeding species.

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A Siblicidal Origin for Avian Brood Parasitism?

Andrew G. Fulmer\textsuperscript{1,2} and Mark E. Hauber\textsuperscript{1,2}

\textsuperscript{1}Animal Behavior and Comparative Psychology, Doctoral Program in Psychology, The Graduate Center, The City University of New York, 365 Fifth Avenue, New York, NY 10016-4309, USA

\textsuperscript{2}Department of Psychology, Hunter College and the Graduate Center, City University of New York, 695 Park Avenue, New York City, New York 10065, USA

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*Correspondence: A.G. Fulmer, Dept. Psychology, Hunter College, 695 Park Avenue, New York, NY 10065, USA

E-mail: afulmer@gradcenter.cuny.edu

Telephone: +1(917) 734-5353
Abstract

We present a model for the evolution of host selection by avian brood parasites from the ecological context of siblicidal brood reduction tactics. Our analysis concentrates on the fitness costs and benefits that permit the evolution of brood parasitism as an adaptive strategy from a state of obligate parental care already featuring siblicide. Limited resources delivered by provisioning parents may incite siblicidal behaviour in offspring, directed towards nestmates regardless of kinship. The extent of siblicidal behaviour (in frequency of occurrence and number of nestmates killed) can extend to the eradication of all nestmates, as has been observed in some raptors and in seabirds. For parents of siblicidal offspring, laying each egg parasitically may maximize offspring survival by eliminating competition between related but siblicidal nestmates. To permit the evolution of conspecific (intraspecific) brood parasitism, costs of siblicide by the offspring of parasitic parents must exceed costs paid by the parasitic parents when losing related conspecifics (host offspring) in a host nest. To permit the evolution of obligate interspecific brood parasitism, costs to fitness from siblicidal offspring or nest reduction of related hosts must exceed costs of heterospecific parental care. Understanding the kin structure between parasites and hosts in conspecific parasitism, and measuring the costs paid by parasitic young due to mismatched incubation, provisioning, and social behaviours by heterospecific foster parents, should provide novel insights into the opportunities and constraints of the evolution of avian brood parasitism.

Keywords Brood parasitism - Nestling competition - Parental care - Siblicide
Zusammenfassung

Liegt im Kainismus der Ursprung von Brutparasitismus bei Vögeln?

Aus dem ökologischen Kontext kainistischer Brutverkleinerungstaktiken heraus stellen wir hier ein Modell für die Evolution der Wirtswahl durch brutparasitäre Vögel vor. Der Fokus unserer Analyse liegt hierbei auf Kosten und Nutzen für die Fitness, welche die Evolution von Brutparasitismus als adaptive Strategie erlauben, ausgehend von einem Zustand obligater elterlicher Brutpflege, bei dem Kainismus (Geschwistertötung) bereits vorkommt. Begrenzte Ressourcen, die von den fütternden Eltern herangeschafft werden, können beim Nachwuchs kainistisches Verhalten auslösen, das sich gegen die Nestgenossen richtet, unabhängig vom Verwandtschaftsgrad. Das Ausmaß des kainistischen Verhaltens (definiert durch Häufigkeit des Auftretens und die Anzahl getöteter Nestgenossen) kann bis zur Auslöschung aller Nestgenossen reichen, wie bei manchen Greifen und Seevögeln beobachtet wurde. Für die Eltern kainistischer Nachkommen kann die parasitische Ablage jeden Eies die Überlebensrate des Nachwuchses maximieren, indem Konkurrenz zwischen verwandten, aber kainistischen Nestgeschwistern ausgeschlossen wird. Um die Evolution konspezifischen (intraspezifischen) Brutparasitismus zu ermöglichen, müssen die Kosten des Kainismus durch die Nachkommen parasitischer Eltern höher sein als die Kosten, welche die parasitischen Eltern zu tragen haben, wenn sie verwandte Artgenossen (Wirtsnachkommen) in einem Wirtsnest verlieren. Um die Evolution obligaten interspezifischen Brutparasitismus zu ermöglichen, müssen die Kosten für die Fitness durch kainistische Nachkommen oder die Gelegeverkleinerung durch verwandte Wirtsvögel die Kosten heterospezifischer elterlicher Brutpflege übersteigen. Das Verständnis der
Introduction

Brood parasitism is a reproductive strategy in which offspring are deposited among the dependent young of another organism. The host organism then pays the costs of raising unrelated young. Brood parasitism has evolved independently in a range of taxa, including insects, fishes and birds, under a wide range of conditions and with diverse natural histories (Johnson et al. 2005; Dierkes et al. 1999; Yom-Tov and Geffen 2006; Kilner and Langmore 2011). A variety of ecological factors (e.g., Krüger and Davies 2002; Yom-Tov and Geffen 2006; Krakauer and Kimball 2009) influence the evolutionary transitions from providing full parental care to completely withholding it, as seen in the handful of obligate avian brood parasites, which comprise less than 1% of all bird species (Cockburn 2006). Specifically, expansion into new habitats with limited or irregularly distributed nesting and foraging resources (Krüger and Davies 2002), as well nestmate killing (siblicide) resulting in brood reduction and competitive advantage to surviving siblicidal offspring (Wang and Kimball 2012), have been proposed as ecological precursors for the evolution of avian brood parasitism. Developmental modality and breeding tactics of hosts, including altricial young and cooperative parental care, have also been shown to enhance the fitness benefits of an already evolved brood parasitic strategy (e.g., Lyon and Eadie 1991; McRae and Burke 1996; Feeney et al. 2013). These life history traits may facilitate brood
parasitism after it has evolved, but are not yet theorized to initiate its evolutionary origin and path. In the paradigm presented by Wang and Kimball (2012), the costs of losing some young to innate siblicidal behaviour could be offset by brood parasitism. Specifically, obligate interspecific brood parasitism (OBP). Nevertheless, not all lineages that display these ecological traits are brood parasites, and some may have had parasitic strategies curtailed by successful host defenses, such as high levels of nest attention and nest defense (e.g., Gonzalez-Martin and Ruiz 1996; Geffen and Yom-Tov 2001; Shaw and Hauber 2012; Feeney et al. 2012). Given the body of research describing evolutionary and ecological similarities between siblicidal and brood parasitic taxa, discussed below, we propose an evolutionary trajectory by which siblicide may be basal to brood parasitism.

The two most common forms of brood parasitism are facultative conspecific brood parasitism (CBP) and OBP. The evolutionary relationship between CBP and OBP has been extensively debated (e.g., Zink 2000; Andersson 2001; Yom-Tov and Geffen 2006; Lyon and Eadie 2008). Potential influences on the type of brood parasitism evolved in a given organism include the relatedness of parasites and breeders within a population (Zink 2000; Andersson 2001), the dynamics of nestmate interactions (Hauber and Kilner 2007; Spottiswoode and Koorevaar 2012), the differential availability of nesting sites (Romagnano et al. 1990), and the developmental modality of hosts and parasites (Lyon and Eadie 2004).

Wang and Kimball (2012) mapped the presence of obligate siblicide in parental avian lineages, and nestmate killing in OBP taxa, onto phylogenies, and found that the OBP clades exhibiting nestmate killing are nested within clades featuring taxa with siblicidal behaviour. For example, the competitive and nestmate-killing parasitic Cuculidae occur in a clade with obligately siblicidal Pelecaniiformes, Sphenisciformes and Gruidae, and that the nestmate-killing
parasitic Indicatoridae appear in a clade with obligately siblicidal Accipitriformes and Strigiformes, as well as an obligately siblicidal hornbill, Bucorvus leadbeateri. The co-occurrence of these traits suggests an evolutionary history for these clades that encouraged extreme levels of nestling competition. Nestling competition for access to parental care is a driving force in the success of both siblicidal and brood parasitic chicks (Lichtenstein and Sealy 1998; Hauber 2003a). In turn, many altricial brood parasites share behavioural and morphological traits with siblicidal taxa; accordingly, the prevalence of bill-hooks and extreme nestmate-directed aggression in Indicatoridae suggests that the clade was basally equipped for siblicide, though it is not known whether this is a cause or effect of brood parasitism (Spottiswoode and Koorevaar 2012).

Wang and Kimball (2012) suggested that instances of discrepancy from their model - for example, the presence of nestmate tolerant lineages in Cuculiformes, including parasitic Cuculidae, may encompass taxa with the potential to become nestmate-killers, but which for a variety of evolutionary reasons have not realized that potential. One such reason is potential size inequality, whereby parasitic chicks larger than hosts will benefit more without having to kill nestmates (Hauber 2003a; Kilner et al. 2004). Wang and Kimball (2012), however, suggest that size inequality alone does not account for all nestmate-tolerant parasites. Other factors considered include the theory that nestmate killing may increase the likelihood of host parents deserting the nest, and this prediction is supported by game theory models. Additionally, and not necessarily alternatively, evolutionary lag may account for some instances of nestmate tolerance: specifically, in species where parasites have only recently evolved a state of OBP (Wang and Kimball 2012). The increase in provisioning based on increased parental stimulation and food solicitation by nestlings, including parasites and hosts (Hauber 2003b), up to a potential
maximum of provisioning may also favor evolution of either tolerance or nestmate killing. This variation would depend on the relative provisioning ability of host parents and the relative stimulating ability of host nestlings to parasite nestlings, called the ‘‘provisions trade-off’’ (Gloag et al. 2012, p. 133). In this way, host-generalists might be either nestmate-tolerant or nestmate-killers, depending on the particular host’s ecology and reproductive strategy (Gloag et al. 2012).

In some cases, a state of context-dependent mutualism may evolve between parasite and host, particularly under conditions of high predation or high parasitism where parasitic chicks have evolved nest defenses that are lacking in their hosts but that are shared with nestmates, including protection from nest predation from which all nestmates (host and parasite) may benefit (Sato et al. 2010; Canestrari et al. 2014). Evidence for an ‘‘egg dilution’’ hypothesis has been found in the parasite–host relationship of Little Bronze Cuckoos Chrysococcyx minutillus and Large-billed Gerygone hosts Gerygone magnirostris (Sato et al. 2010). Large-billed Gerygones evict parasite young, but not parasite eggs. In this instance, the presence of a parasite egg may preclude multiple parasitism on the same nest. Small clutch size and high parasitism rates are suggested as the necessary conditions for this system (Sato et al. 2010). The Great Spotted Cuckoo Clamator glandarius is nestmate tolerant and able to produce a secretion that appears to reduce predation in hosts (Canestrari et al. 2014). Though parasite presence in the nest reduces the number of host young successfully fledged, it does not appear to reduce the condition of surviving host young. Similarly, this system makes parasites beneficial to hosts under conditions of high predation (Canestrari et al. 2014). The evolutionary trajectory presented here attempts to characterise the conditions under which siblicide may create a ‘‘predisposition’’ (Wang and Kimball 2012, p. 828) to either type of brood parasitism (Fig. 1).
Brood parasitism may be linked to siblicide as a function of parent-offspring conflict. Theoretical models (Mock 1987; Parker and Mock 1987; Godfray et al. 1991) propose that siblicide is (largely) the result of selection on offspring as opposed to parents, since siblings and parents may be differently affected by parameters of optimal clutch size. When resources are unpredictable, optimal clutch size for offspring may be smaller than the optimal clutch size for a parent. In this scenario, a parent benefits from the bet-hedging strategy of more offspring, while offspring would benefit from being the sole focus of parental care (Godfray et al. 1991). When multiple nestlings cannot be supported in a single nest, brood parasitism may be a mechanism for parents to retain some benefits of producing a larger clutch size than what is optimally cared for in a single nest (McRae 1998). Such a strategy would also prevent offspring from competing with close kin, as their nestmates would be much less closely related than full siblings, even in populations featuring related parents nesting nearby (Andersson 2001).

Yom-Tov and Geffen (2006) suggest that altricial species more often engage in the OBP strategy and precocial species more often engage in CBP, though whether a parasitic species is altricial or precocial does not exclusively determine its type of parasitic strategy (but see Lyon and Eadie 2008). Exceptions to this pattern include the OBP Black-headed Duck *Heteronetta atricapilla*, which is precocial, and the North American cuckoos *Coccyzus americanus* and *C. erythropthalmus*, which engage in facultative OBP (Robert and Sorci 2000; but see Dearborn et al. 2009). Models for the evolution of brood parasitism as a stable strategy that incorporate socio-ecological factors (including resource access and kinship level: Lyon and Eadie 2004; Kilner and Langmore 2011) often feature ontogenetic, morphological, and behavioural traits relevant to sibling competition. For example, taxa with either brood parasitism or brood reduction share nestling traits such as competitive begging, asynchronous hatching, aggression
against nestmates, and eviction or displacement of nestmates (Bischoff and Murphy 1993; Moskat and Hauber 2010; Spottiswoode and Koorevaar 2012). Dependence on parental care is necessarily greater in species with altricial than in species with precocial ontogenies, and so precocial species do not need to compete as strongly for parental attention and provisions (Robert and Sorci 2000). Altricial taxa might make greater use of these competitive tactics within the nest than precocial species, which in turn do not necessarily benefit to the same extent from monopolizing parental care.

Depending on the particular taxon, CBP may present itself as relatively rare, best-of-a-bad-job reproductive strategy, compared to full parental care (McRae 1998; Anderholm et al. 2009; Shaw and Hauber 2009, 2012; Shaw et al. 2014). The origin of CBP in this form likely stems
Fig. 1 Linking siblicide and brood parasitism with ecological constraints
Key
Arrows indicate evolutionary trajectories
Rectangles indicate given phenotypic or ecological states
“c” indicates fitness cost
“r” indicates relatedness
“e” indicates energy expended

from nest loss or other “accidental” causes, including the misidentification of own nests (Robert and Sorci 2000) and may result in the recovery of some of the energetic investment directed into developing eggs en route to the oviduct (e.g., Hamilton and Orians 1965; Shaw et al. 2014).

Theoretically, CBP need not be a superior reproductive strategy to be evolutionarily stable (Nee and May 1993), especially if it is constrained by individual quality and variation in access to resources. For example, if individuals that are unable to successfully compete for limited resources in a patch are able to engage in reproduction via nest parasitism of conspecifics, the CBP trait will persist in the population. If resources are unpredictable, individuals of higher competitive quality will, by definition, monopolize them. Individuals of lower competitive quality, but with the capacity to parasitize, will achieve some level of reproductive fitness and will outcompete some (but not all) higher competitive quality individuals that lose in competitive interactions but do not engage in parasitism.

Another trajectory for CBP evolution, not mutually exclusive from that seen above, is based on a genetic argument. Amongst altricial birds, low-skew male biased incubators are disposed to communal breeding with some degree of CBP (Vehrencamp 2000; Geffen and Yom-Tov 2001; Riehl 2010). The Common Eider Somateria mollissima, a species that practices CBP, preferentially selects kin as hosts over nearer neighbors (Waldeck et al. 2007), and some models claim that facultative CBP of kin can be advantageous to both parasitic and host females if the costs of raising a parasite are relatively low (e.g., Andersson 2001; Lopez-Sepulcre and Kokko
This is because inclusive fitness advantages may offset costs of raising a parasite (Andersson 2001). However, in another lineage with CPB, the Goldeneyes *Bucephala spp.*, the fitness effects of such kin biased parasitism show mixed effects and vary based on spatial and genetic dimensions of relatedness and ecological variation in nesting opportunities (Pöysä 2004; Eadie and Lyon 2011).

CBP is less likely to be fatal to all host-offspring, as the resource demands of a conspecific (and synchronously hatched) parasite are logically no greater than the resource demands of offspring. Additionally, conspecific parasites may share alleles with host parents, further lessening the costs to CBP hosts compared with nestmate-killing OBP hosts (Hamilton and Orians 1965; Andersson 2001). Similar strategies have been observed in American Coots *Fulica americana* (Lyon 2007).

Decreases in the optimal clutch size in the genetic parent’s nest following the evolution of CBP tactics (which permit the spreading of eggs across multiple nests) could facilitate evolution of OBP (Godfray et al. 1991; Robert and Sorci 2000). Support for this negative association between optimal clutch size per nest and increased parasitism by females with committed eggs comes from several species, including European Starlings *Sturnus vulgaris*. Romagnano et al. (1990) showed that European Starlings may adopt a strategy of laying one egg less than the optimal clutch to compensate for potential CBP. Some colonial species may parasitize nests to lay physiologically committed eggs, in the absence of an available nest (i.e., due to nest predation) (Hamilton and Orians 1965; Yezerinac and Dufour 1994; McRae 1998; Shaw and Hauber 2009, 2012, but see Rothstein 1993). Cues about environmental risks to brood survival, such as variable or limited food availability, nesting territory stability, and climatic cues, are likely to be equally available and assessed by host and parasite when the two occupy the same population. Much of the information above offers a compelling set of connections between siblicide and
avian brood parasitism. Our model integrates that information. We highlight similarities in the occurrence of both siblicidal and brood parasitic strategies (that they may be exhibited as a response to fluctuations in resource availability) and similarities in costs and benefits that must be negotiated on both evolutionary trajectories. We suggest that siblicidal tactics may have been basal to some avian brood parasite lineages, and attempt to show the most parsimonious model for this evolution. The prediction is that under the conditions described below (see Fig. 1), avian populations experiencing high competition for nest space and fluctuations in resources between breeding events (Fig. 1a, b), and brood reduction will evolve (Fig. 1d). When brood reduction takes the form of siblicide and the fitness inequalities expressed in Fig. 1 are present, brood parasitism becomes a stable strategy. We predict that transitions between CBP and OBP should be moderated by the availability of an appropriate host - in our model, such a host must have sufficiently similar needs (in terms of nutrition, nesting habits, location, and other ecological traits), and the shared alleles of conspecific eggs to the parasite, which would be lost in a CBP scenario, must be lower than the shared alleles of own-eggs lost to any incompatibilities in ecological need with a heterospecific host (Fig. 1n).

Model

Assumptions

Fluctuation in resource availability is necessary for a dissonance between evolved laying capacity and optimal clutch size. This is because under unpredictable conditions, some breeding
events will occur at times when more than one chick may be supported, while others occur when only one can survive (e.g., Bortolotti 1986; Anderson and Ricklefs 1992). Siblicide will then be likely to evolve facultatively when these shortages occur (as in food and nesting substrate/space, or other ecological resources that may be necessary to support the optimal clutch size for specific taxa). In turn, obligate siblicide will evolve when these shortages represent predictable ecological conditions. Specifically, where optimal clutch size is different for the parent versus offspring, obligate siblicide may evolve as a result of ecological selection, impacting offspring rather than parents (Godfray et al. 1991).

The first assumption of our trajectory (see Fig. 1a) is an inequality between competitors and nesting territories. We also assume that factors including natal dispersal, breeding site fidelity, and seasonal migratory habits will affect this inequality and in turn be affected by it (Fig. 1c). Breeding site fidelity may be an adaptive tactic for brood parasites, permitting monopolization of hosts and access to naïve breeding-site faithful hosts at their first nesting attempt, possibly increasing the chances of egg acceptance in subsequent nesting attempts by the same individuals (Hauber et al. 2012). Krüger and Davies (2002) found that shifts by parental care-providing ancestors from year-round to more seasonal breeding territories may be a precursor to the evolution of brood parasitism in at least the three cuckoo clades in which parasitism has evolved independently. Because species without an evolutionary history as hosts may lack evolved defenses against parasites (Hoover 2003), immigration to new areas may present an opportunity for parasitism at comparatively low rejection costs. Predictably stable coevolutionary cycles between brood parasites and hosts are relatively rare compared with successful parasitism (lack of rejection by hosts) or unsuccessful parasitism (consistent rejection by hosts) (Soler 2014). Soler (2014) also suggests that as the host-parasite arms race reaches one of the latter two states
(consistent acceptance or rejection of parasites), then switching by the parasite to new 
evolutionarily naïve hosts may prove more adaptive than previously used hosts, which are most 
adaptive to be used only under conditions of low parasitism rates. By the same token, migration 
to novel environments may facilitate the use of naïve hosts and, subsequently, successful parasitism (Soler 2014).

Variation in these same factors, exhibited by both parasite and host, have also been shown to 
influence the arms race between parasite strategy and host defense (Hoover and Hauber 2007; 
Saino et al. 2009; Møller et al. 2011). Natal philopatry in hosts may lead to the intergenerational 
transmission of parasitic egg acceptance; among Prothonotary Warblers Protonotaria citrea, 
daughters raised in nests with parasites were more philopatric and likely to be parasitized 
themselves than their counterparts raised without parasites (Hoover and Hauber 2007). The reuse 
of nests within a season provides brood parasites multiple opportunities to parasitize a known 
location; some species of brood parasites have, in turn, evolved strategies to manipulate 
renesting behaviour of hosts, such as ‘mafia’ and ‘farming’ tactics (Hoover and Robinson 2007; 
Hauber 2009). Changes in climate have been shown to impact the timing of parasitic behaviour 
relative to host laying, as populations of hosts move or expand their range (Saino et al. 2009; 
Møller et al. 2011). Brood parasites may be effective invaders due to their ability to lay eggs far 
from their own feeding sites, adding another layer of feedback from migratory habits (Krüger 
and Davies 2002).

In this model, we focus on the necessary transitions for an evolutionary trajectory from siblicidal 
to brood parasitic tactics. We do not differentiate between the developmental strategies of 
precocial and altricial taxa. We propose that it is the relative fitness inequalities between parental 
care strategies and parasitism that remain critical to the evolution of brood parasitism in both
types of taxa, though the absolute values substituted for the variables (see Fig. 1) may differ dramatically between altricial and precocial species.

**The role of kinship**

Parental care strategies may be affected by the relatedness between all members of a breeding population, including nonbreeding individuals (helpers). Helpers at the nest may be involved not only in raising related chicks, but also in depredating foreign chicks (Eberhard 1975; De Mársico et al. 2012). The fitness equations we propose as links between siblicidal and brood parasitic systems concern inclusive fitness metrics (Hamilton 1964) as a determining variable in the relative costs and benefits of adopting a brood parasitic strategy (e.g., Zink 2000; Andersson 2001; Eadie and Lyon 2011). Consequently, our first prediction is that the degree of relatedness of conspecific eggs in the host nest must be less than the aggregate relatedness of offspring lost to siblicide (Fig. 1e). Under these conditions, CBP, which may occur variably among members of a population, would be selected over siblicidal tactics. Members of a breeding population that experiences fluctuating resources (Fig. 1f, g), with occasionally insufficient levels to maintain optimal clutch size, will be selected for the strategy which best permits consistent “testing” of facultative brood reduction strategies (Clutton-Brock and Parker 1995). This facultative “testing” system is similar to the asymmetric aggressive retaliation between dominant and subordinate members of stable social groups (a type of spite: Jensen 2010). These tactics will manifest as CBP only when the net loss to fitness from parasitizing a potentially closely related conspecific is less than the net loss from siblicide among offspring (Fig. 1e).

We propose that three major fitness conditions are necessary to be met for OBP to be favored.
First, a sympatric heterospecific host (which by definition has lower relatedness than any conspecific) must be readily and abundantly available (Fig. 1m). Second, a variety of risks and costs are posed to the parasitic chick from heterospecific parental care, such as improper nutrition, incubation, socialization or the effects of nestling competition (Petrie and Møller 1991; Yang et al. 2013). These costs must be less than the cost incurred to the parent by siblicidal offspring (Fig. 1n). Third, the risks and costs posed to the parasitic chick, and by extension, fitness costs to the parasitic parent, from heterospecific parental care, must be less than the cost to the parasite parent from the loss of potentially related conspecific eggs (of the host) incurred by the presence of brood parasitic offspring (Fig. 1o). This context permits a mechanism for solitary nesters to adopt a brood parasitic tactic, as the degree of sociality and population spatial structure are severely limiting constraints on the net gain from CBP strategies (Geffen and Yom-Tov 2001). It is expected that the values of the variables provided in these inequalities will be very different according to ecological circumstance, reflecting further diversity in brood parasitic tactics along dimensions such as the frequency and number of nestmates eradicated and host-specialization (Kilner 2005).

**Ecological mechanisms favoring parasitism over alternative strategies**

Selective pressures on an altricial taxon to adapt to new niches could parallel those that have been put forward as selectors for brood reduction strategies. For example, floating European Starling females parasitize conspecifics as an alternative strategy to nesting on their own (Lombardo et al. 1989; Sandell and Diemer 1999), a potentially adaptive behaviour in a novel and/or resource-limited habitat patch following dispersal. The adaptation to new food sources is
closely linked with limitation of prior food sources, which might lower the number of
supportable offspring (and trigger facultative siblicide), or produce asynchronous hatching and
high sibling aggression (Stouffer and Power 1990; Romagnano et al. 1990; Robert and Sorci
2000). If optimal clutch size still exceeded the number of siblings that could be supported in a
given nest, either CBP or OBP could become a profitable alternative strategy (Godfray et al.

For brood parasitism to evolve from siblicide, costs of siblicide to the parent must also be greater
than costs of multiple-nest parasitism. Such a structure could arise from asynchronous hatching
strategies associated with brood reduction, which would yield the laying of eggs into multiple
nests by the same female. Tending nests used by multiple females has evolved in several
ecological contexts and evolutionary lineages, with varying skew in care-taking behaviour,
reflective of the potential continuum of brood care strategies, including, but not limited to, CBP,
cooperative breeding, and communal breeding, as detailed in Lyon and Eadie (2008). Avian
female–female dyads providing cooperative biparental care are believed to occur most frequently
in seabird populations as an alternative brooding strategy. Among such populations, female–
female parental dyads are relatively common. About 14 and 31 % respectively of focal nesting
populations of Western Gulls *Larus occidentalis* and Laysan Albatross *Phoebastria immutabilis*
exhibit this form of biparental care, respectively. It occurs also among Roseate Terns *Sterna
dougallii* and California Gulls *Larus californicus* (Hunt and Hunt 1977; Young et al. 2008;
Bailey and Zuk 2009). In this strategy, only one nest is used for the offspring of one or more
Larus species, *Phoebastria immutabilis*, and *Sterna dougalii* females at a time. Communally
nesting Acorn Woodpecker *Melanerpes formicivorus* and Pukeko *Porphyrio porphyrio* females
also tend nests in dyads, but distribute care asymmetrically (Vehrencamp 2000), a trait consistent
with CBP. Extrapair paternity is seen in 25 % of nests (and 14 % of chicks) among Superb Starlings *Lamprotornis superbus*, but CBP has not been detected (Rubenstein 2007). If fledging survival is determined by provisioning and protection, while hatching survival is determined primarily by incubation, optimal clutch size may be lower for a species when CBP occurs in the population (Vehrencamp 2000). Female–female nesting pairs among the Laysan Albatross attend to only one egg per year, but provide roughly equal opportunity to raise each individual’s offspring by nesting repeatedly (Young et al. 2008). As with CBP (McRae 1998; Anderholm et al. 2009), homosexual biparental care has been considered an alternative strategy yielding lower reproductive success than heterosexual biparental care (Bailey and Zuk 2009). These lines of evidence hint that CBP and communal nesting may both be alternative adaptations to shared socio-ecological conditions.

**Conclusion**

Our proposed model accounts for broad fitness effects, focusing on the ultimate causes of brood parasitism in terms of inclusive fitness. Prior models did not fully integrate variables of relatedness and energetic costs/resource availability when considering the evolution of parasitism, and instead focused on one or the other (e.g., Krüger and Davies 2002; Lopez-Sepulcre and Kokko 2002; Yom-Tov and Geffen 2006). This model is intended to apply with similar applicability to precocial and altricial taxa. The three inequalities associated with differential relatedness seem likely to be essential components of evolving a brood parasitic strategy from parental care with siblicidal young. First, in the transition to CBP strategies from brood reduction through siblicide, the cumulative relatedness (Hamilton 1964) between parents
and host nestmates lost to siblicidal offspring must be lower than the cumulative relatedness between parents and own offspring endangered by remaining with (or being raised alongside) nestmate-aggressive siblings. Second, in the transition from siblicidal tactics to OBP, the cumulative relatedness to the parent of offspring lost to sibicide must be greater than the cumulative relatedness to that parent of parasitically deposited offspring lost to host negligence, eviction/injury and/or care-strategy incompatibilities (including, nutritional differences and incubation differences between host and parasite). Third, for OBP rather than CBP to evolve, the cumulative relatedness of conspecific eggs that might be endangered by the deposition of a parasitic offspring in their nest must be greater than the cumulative relatedness to the parasitic parent of chicks lost to the costs of heterospecific parental care.

Brood parasitism is a coevolutionary process (Rothstein 1990; Kilner 2005), and so a more complete modeling approach should include the various host traits that are altered following the onset of parasitism and which reciprocally affect the brood parasites’ behaviours in an ongoing arms race of different sequences and paces of adaptations and counteradaptations.

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**Compliance with ethical standards**

**Conflict of interest** The authors declare that they have no conflict of interest.
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Mock DW (1987) Siblicide, parent-offspring conflict, and unequal parental investment by egrets


Intrabrood rank, age, and adult presence predict novelty-seeking in individual Arabian Babblers (*Turdoides squamiceps*)

A.G. Fulmer\textsuperscript{a,*}, P. Santema\textsuperscript{b}, and M.E. Hauber\textsuperscript{a,\textasciicircum{c}}

\textsuperscript{a} Animal Behavior and Comparative Psychology, Doctoral Program in Psychology, The Graduate Center, The City University of New York, 365 Fifth Avenue, New York, NY 10016-4309, USA

\textsuperscript{b} Department of Behavioural Ecology & Evolutionary Genetics, Max Planck Institute for Ornithology, Eberhard-Gwinner-Strasse 7, 82319, Seewiesen, Germany

\textsuperscript{c} Department of Psychology, Hunter College and the Graduate Center, City University of New York, 695 Park Avenue, New York City, New York 10065, USA

*Correspondence: A.G. Fulmer, Department of Psychology, Hunter College, 695 Park Avenue, New York, NY 10065, USA

E-mail: afulmer@gradcenter.cuny.edu

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Abstract: Risk taking and neophilia affect many aspects of an individual's life trajectory, including social rank, philopatry, reproductive success and mortality. We investigate mechanisms by which early life socialization may have lasting impacts on behaviours across contexts by assessing the relationship between social rank and neophilia at different stages of development. In the cooperatively breeding Arabian babbler, *Turdoides squamiceps*, age is positively correlated with dominance and reproductive skew. Early life socialization, here represented by social rank order relationship to clutch-mates, may provide a major additional source of variation within age cohorts in overall social opportunities and the resulting reproductive strategies. We test the hypothesis that novelty-seeking behaviour is related to intrabrood rank in Arabian babblers; we presented familiar versus novel stimuli (stationary objects, moving objects and sounds) to birds. To examine intrabrood dominance as a potential predictor of later-life neophilic behaviours, we constructed a multimodal index of novel stimulus approach behaviour for fledglings and juveniles living in an individually marked population, and compared it against an intrabrood rank metric based on scramble competition (rank index) to allow comparisons between different broods and groups. All birds were more likely to react to novel stimuli than to familiar stimuli. Intrabrood rank index positively predicted the frequency of novel stimulus approach, with individuals of higher intrabrood rank more frequently approaching novel stimuli. Juveniles made more approaches to novel stimuli and made those approaches earlier in the trial than did fledglings; approaches by all young birds were more frequent when an adult was present versus absent at the beginning of the presentation. These findings suggest an interaction between novelty-seeking behaviour by young birds and displays related to social rank and/or competitive ability. In this way, novelty-seeking behaviours in early life may be connected with lifetime social and reproductive trajectory.
Introduction:

Risk taking and neophilic behaviour, plastic or chronic, may influence reproductive opportunities and lifetime fitness (Boissy, 1995; Smith & Blumstein, 2008). Among birds, intraspecific variation in neophilic behaviour has been linked to ecological plasticity, learning speed and innovation (Greenberg & Mettke-Hofmann, 2001). Self-exposure to novel stimuli is, by definition, a gamble and constitutes a strategic choice (Boissy, 1995; Greenberg & Mettke-Hofmann, 2001). Neophilic behaviour can be a facultative strategy when resources fluctuate to permit information gathering (Greenberg & Mettke-Hofmann, 2001), and it has been linked to social rank and experiential outcomes of social conflict in a wide variety of taxa, including fish (e.g. Frost, Winrow-Giffen, Ashley, & Sneddon, 2007), birds (e.g. David, Auclair, & Cézilly, 2011; Stöwe et al., 2006) and mammals (Chamove, 1983).

The direction of the relationship between novel stimulus approach and social rank is not uniform among bird species or even within species (Boogert, Reader, & Laland, 2006; David et al., 2011; Dingemanse & de Goede, 2004; Stöwe et al., 2006). Neophilic behaviour has been found to be either positively or negatively associated with social dominance, depending on the ecological and social context (Dingemanse & de Goede, 2004; Greenberg & Mettke-Hofmann, 2001; Stöwe et al., 2006). Among zebra finches, Taeniopygia guttata, neophobia has a strong negative relationship with social dominance (David et al., 2011). Adult male great tits, Parus major, with established territories are quicker to explore a new territory and are also more socially dominant (Dingemanse & de Goede, 2004). In turn, among younger male great tits without established territories, subordinate individuals are quicker to explore (Dingemanse & de Goede, 2004). Finally, when pairs of male ravens, Corvus corax, were exposed to novel objects, the subordinate member of the pair was the first to approach the novel object, whereas in mixed-
sex dyads, dominants approached the novel object first (Stöwe et al., 2006). In contrast, Stöwe and Kotrschal (2007) found no effect of social rank on novel object approach in ravens.

It has been suggested that subordinate individuals are more likely to take risks in foraging, driven by lower resource access than dominant individuals (Bergmüller & Taborsky, 2010). According to this theory, socially subordinate individuals should have shorter latencies to approach novel objects, as dominant individuals are capable of monopolizing the resource even if they approach later (Boogert et al., 2006). Alternatively, if novel objects are inherently appealing, or if subordinates experience social inhibition in the presence of dominants (Stöwe et al., 2006), socially dominant individuals will monopolize novel resources.

The Arabian babbler, *Turdoides squamiceps*, is a cooperatively breeding bird that lives in highly exclusive social groups with a fixed hierarchy (Kalishov, Zahavi, & Zahavi, 2005; Zahavi, 1990). Age appears to be strongly and positively correlated with social dominance and reproductive skew in babbler groups (Zahavi, 1990), making the competitive relationships among brood-mates and group composition during early life a major potential source of individual variation in social experience and strategy, including succession to social dominance. Within clutches (age cohorts), the apparent social dominance structure is the result of competition in the first few weeks of life (Zahavi, 1990). Food division among nestlings, which may influence competitive ability, appears to be determined (cyclically) by clutch-mate competition rather than by hatch order, although if older individuals are experimentally cross-fostered, they appear to have greater competitive ability (Ostrieher, 1997). We investigated the role of ontogeny by focusing on the predictive effects of intrabrood rank on novel stimulus approach in early life for this cooperative breeding species (Bergmüller & Taborsky, 2010).

Social facilitation of novel object investigation may or may not depend on prior
experiences; for example, observing the interaction of a conspecific with an uncertain or potentially risky stimulus can be a useful form of risk avoidance (Griffin & Boyce, 2009). In turn, the quality or nature of a new food item, or a new mechanism for acquiring a food item, can also be socially transmitted (Fritz & Kotrschal, 1999; Langen, 1996). Individual differences in producer/scrounger tactics and innovations in foraging strategy have been associated with adult breeding rank in Arabian babblers: adult subordinates (nonbreeders) are more likely to find food by observing food-finding behaviours of dominants rather than by finding food themselves (acting as scroungers) and they are faster to innovate foraging strategies than dominants (Keynan, Ridley, & Lotem, 2014). An important influence on the behaviour of young individuals is the observation of adult behaviour. We therefore also examined the relationship between adult presence or absence and investigation of novel stimuli by young.

Our aim in the present study was to determine whether an individual's social rank influences its likelihood of approaching stimuli of uncertain resource value, and thus, to distinguish between two hypotheses: the risk-averse hypothesis and the risk-seeking hypothesis. (1) In the risk-averse hypothesis, novel stimuli are potentially threatening, and subordinates will approach more frequently and/or more quickly than dominants, which have greater access to food and other resources (resource access) and do not need to take such risks (Laland & Reader, 1999; Thompson et al., 2013). (2) In the risk-seeking hypothesis, individuals are attracted to novel stimuli as potentially valuable resources worth monopolizing. Monopolization of items of uncertain value, or repeated approach, may also be a result of a winner effect (Frost et al., 2007), or an honest signal of ability. In this model, dominant individuals will approach more frequently and/or more quickly than subordinates, as an extension of the greater resource access exercised by dominants. We set out to address the way in which early life intrabrood social rank, a measure
of early life sibling social relationship, may relate to the perceived risk or reward value of novel object approach, an inherent gamble.

To comprehensively assess approach to different types of novelty, we presented both stationary and moving objects as well as acoustic stimuli to babbler groups. Each stimulus modality (stationary, moving, acoustic) had a familiar and a novel stimulus type, resulting in six test stimuli. The order of presentation was included as a potential confound in our models. Our statistical models also accounted for potential effects or confounds of a variety of individual traits, sex ratio, sex, age class (fledgling/juvenile) and group size on the frequency and latency to approach novel stimuli.

METHODS

Subjects

Subjects were free-living Arabian babblers from two age groups: 19 juveniles (3-11 months old; mean age = 163 days, range 93-246 days) from six groups; 13 fledglings (<3 months old; mean age = 26 days, range 15-34 days) from four groups. The sex of some birds was unknown because of disappearance/mortality before the age of conspicuous sexual dimorphism. All individuals in the study occupied mixed-sex groups at the time of the trials. The birds were studied in the Shezaf Nature Reserve in the Negev Desert near Hazeva, Israel. The population has been the focus of an ongoing study organized and maintained by Professors Amotz and Avishag Zahavi (e.g. Zahavi, 1990) and their research group for 40+ years. All birds in the study area are habituated, banded and censused on a regular basis. Banding of nestlings occurs at approximately 8 days of age. Habituation includes presentation of food items (mealworms and/or bread) to individuals on a regular basis.

Intrabrood Rank Testing: Paired Scramble Competition
To establish intrabrood ranks, the standard protocol involves presentation of one live mealworm to two young (<5 months old) situated approximately equidistant from and within 1 m of a seated observer (method adapted from Carlisle & Zahavi, 1986). The winner and the social aftermath (i.e. the outcome of the next interaction between participants within 15 s) are then recorded for each individual. We also established a simple dominance index to permit comparison of relative social rank among birds of different clutches and groups: number of wins/number of surviving clutch-mates. We generated this index for each individual relative to members of its own clutch to better separate the effects of intrabrood rank and interbrood rank (age-based dominance). Hatch order within clutches was not known.

**Novel/Familiar Stimulus Approach Experiment**

**Presentations**

All stimuli were presented to each group (and consequently to all individuals) on 5 different days (see Table 1). During each session, all six condition types were presented in a randomized order (random.org) over a 2 h period.

Prior to initiating experimental presentations for each group, the presenter (A.G.F.) waited at least 15 min while in proximity of

**Table 1. Presentation types**

<table>
<thead>
<tr>
<th>Modality</th>
<th>Trial Class</th>
<th>Stimulus</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stationary object</td>
<td>Familiar</td>
<td>Rock</td>
<td>Ovoid. ~ 10 x ~ 6.5 x 3 cm.</td>
</tr>
<tr>
<td>Type</td>
<td>Familiarity</td>
<td>Description</td>
<td>Remarks</td>
</tr>
<tr>
<td>----------------------</td>
<td>-------------</td>
<td>--------------------------------------</td>
<td>----------------------------------------------</td>
</tr>
<tr>
<td>Stationary object</td>
<td>Novel</td>
<td>Kitchen sponge</td>
<td>Rectangular. Iridescent blue and silver. 8.25 x 10.8 x 2 cm.</td>
</tr>
<tr>
<td>Moving object</td>
<td>Familiar</td>
<td>Leaves (moved with dental floss string)</td>
<td>End of a date palm frond with leaves, found on the reserve. ~17 x 12 cm. POH Dental Floss: “No Wax™ Classic 490</td>
</tr>
<tr>
<td>Moving object</td>
<td>Novel</td>
<td>Plastic rectangle (moved with dental floss string)</td>
<td>Yellow. 19 x 11.5 cm. POH Dental Floss: “No Wax™ Classic 490</td>
</tr>
<tr>
<td>Acoustic</td>
<td>Familiar</td>
<td>Recording of white spectacled bulbul (Pycnonotus xanthropygos)</td>
<td>30 second playback repeated through trial. These birds coexist with the study population and are relatively common on the reserve.</td>
</tr>
</tbody>
</table>
**Acoustic Novel Recording of 30 second playback**

- “Pennsylvania 65000” from the Glenn Miller album
- “Pure Gold”

Unfamiliar anthropogenic sound arrangement.

the group (<10 m from at least one individual most of the time) until the birds resumed normal foraging behaviour. Each stimulus presentation lasted 1 min from the beginning of data collection to the end, with at least 10 min between presentations to permit the birds to return to their normal foraging state (as subjectively assessed by observer) within ~10 m of the presenter. When all juveniles or fledglings were within ~5 m of one another, and within ~10 m of the presenter, stimuli were deployed. After deployment, the presenter slowly moved away from the stimulus to a distance of 5 m (as calculated by eTrex GPS). Although the birds were exposed to stimuli during this period, recording did not begin until the observer was in position. The stimulus and the area surrounding it (<30 cm) were observed through binoculars to accurately assess each participating bird's ID (colour ring).

*Test stimuli*

*Stationary.* Objects were deployed by hand.

*Moving.* Objects were deployed by hand, then slowly pulled towards the observer in random trajectories using dental floss string tied to the object.

*Sound.* Two sounds were played at identical volume settings and peak amplitudes from an iPod 4TM connected to an X-Mini II XAM4-B Portable Capsule SpeakerTM. Both speaker and iPod were covered in cloth and concealed in sand to standardize and mitigate visual interference in the
acoustic signal. The sounds were audible to the observer at 5 m.

**Data Collection**

Data were collected during September-November 2013 (juveniles) and March-May 2014 (fledglings). Observations began when the observer was positioned at 5 m distance. No approaches made by birds while the observer was in motion were recorded. A record was made if an adult was standing within ~30 cm of the stimulus at the beginning of a given session. Each approach (defined by movement towards the stimulus within ~30 cm) by a juvenile or fledgling was recorded.

**Analysis**

The average latency to first approach was calculated for each bird, along with the average frequency of approach to each stimulus per trial (the number of times an individual came within ~30 cm of the stimulus). A general linear model is presented, in which we used a backward elimination procedure (Grafen & Hails, 2002). We used trial modality (stationary object, moving object, acoustic playback), trial class (familiar/novel), order of presentation (order in which stimuli of each modality/class were presented), adult presence (within 30 cm of the stimulus at the beginning of a session), age class (fledgling/juvenile), group size, individual ID, clutch ID, sex, sex ratio and intrabrood rank as predictor variables, and frequency and latency as response variables (in separate tests). Sex was excluded from the analysis but included in the lack of fit. Trial modality, individual ID and clutch ID were random effects. We removed the least significant nonsignificant predictor from each model, resulting in a reduced model with significant predictors and the predictor of main interest: treatment. This treatment predictor was retained in the model regardless of its significance. Full and stepwise reduced models are presented (see Results). Analyses were performed in SAS/JMP 11 statistical software (SAS
Institute, Cary, NC, U.S.A.).

**Ethical Note**

Procedures unique to this research, in addition to the general practices of the Arabian Babbler Project, Tel Aviv University (Zahavi, 1990), were approved by the Institutional Animal Care and Use Committee of Hunter College, City University of New York (New York, NY, U.S.A.; protocol number MH-social 2/18/01). No stimuli resembled or simulated predators. Individuals were identified with unique combinations of coloured rings on their legs (each ring was ~0.5 cm in width).

Table 2. Latency to approach: predictor effects

<table>
<thead>
<tr>
<th>Fit Model</th>
<th>Least significant predictor</th>
<th>Effect size</th>
<th>SE</th>
<th>df</th>
<th>P</th>
<th>Wald statistic</th>
</tr>
</thead>
<tbody>
<tr>
<td>Full Model</td>
<td>Rank index</td>
<td>-0.164</td>
<td>1.114</td>
<td>1</td>
<td>0.882</td>
<td></td>
</tr>
<tr>
<td>2nd Model</td>
<td>Order of presentation</td>
<td>-0.129</td>
<td>0.377</td>
<td>1</td>
<td>0.731</td>
<td></td>
</tr>
<tr>
<td>3rd Model</td>
<td>Adult presence</td>
<td>0.303</td>
<td>0.720</td>
<td>1</td>
<td>0.673</td>
<td></td>
</tr>
<tr>
<td>4th Model</td>
<td>Age class*Trial class</td>
<td>-0.533</td>
<td>1.080</td>
<td>1</td>
<td>0.621</td>
<td></td>
</tr>
<tr>
<td>5th Model</td>
<td>Sex ratio</td>
<td>-1.072</td>
<td>1.811</td>
<td>1</td>
<td>0.555</td>
<td></td>
</tr>
<tr>
<td>6th Model</td>
<td>Age class*Rank index</td>
<td>1.097</td>
<td>0.794</td>
<td>1</td>
<td>0.185</td>
<td></td>
</tr>
<tr>
<td>7th Model</td>
<td>Trial class</td>
<td>1.172</td>
<td>0.784</td>
<td>1</td>
<td>0.136</td>
<td></td>
</tr>
<tr>
<td>8th Model</td>
<td>Group size</td>
<td>0.592</td>
<td>0.327</td>
<td>1</td>
<td>0.094</td>
<td></td>
</tr>
<tr>
<td>Minimal Model</td>
<td>Age class</td>
<td>7.601</td>
<td>1.004</td>
<td>1</td>
<td>&lt; 0.0001</td>
<td>7.57</td>
</tr>
</tbody>
</table>

Table 3. Latency (s) to approach: fitted models

<table>
<thead>
<tr>
<th>Fit Model</th>
<th>Predictor removed to</th>
<th>$r^2$ adjusted</th>
<th>RMSE</th>
<th>P</th>
</tr>
</thead>
</table>

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### Results

**Predictors of Latency to First Approach**

The full model included all predictors (Tables 2-4). The least significant predictor (rank index) was then removed. The least significant predictor in the revised model was the order of presentation, which was also removed. The third fit showed the least significant predictor to be adult presence. The fourth model excluded adult presence. The least significant predictor was age class by trial class. A new model excluded age class by trial class. The least significant predictor in this model was sex ratio, which was excluded from the subsequent model. The resulting model revealed age class by rank index as the least significant predictor. The new model excluded age class by rank index and showed the least significant predictor to be trial class. A fit excluding trial class showed that group size tended towards significance as a positive predictor of latency to first approach.

The final model retained only age class as a predictor of latency to first approach. Juveniles were significantly quicker to approach stimuli than were fledglings (Fig. 1).

**Predictors of Approach Frequency**
The full fitted model included all predictors (Tables 5-7). The least significant predictor (group size) was removed. The least significant predictor in the revised model was order of presentation. The third fit contained only one nonsignificant predictor: sex ratio. Sex ratio was removed, resulting in the final model that included rank index, trial class (familiar/novel), adult presence at the beginning of the trial, age class (with the nested predictor: sex), age class by trial class and age class by rank index. Young Arabian babblers preferentially responded to novel stimuli: novelty (versus familiarity) was a positive predictor of approach frequency (Fig. 2). Intrabrood rank positively predicted frequency of approach (Fig. 3). Juveniles were more likely to approach stimuli than were fledglings (Fig. 2). The presence of an adult at the beginning of a trial increased the frequency of approach (Fig. 4).

DISCUSSION

We found support for a risk-seeking hypothesis across family groups of Arabian babblers. Latency to first approach of all stimuli

Table 4. Covariance Matrix of Component Estimates: latency to approach

<table>
<thead>
<tr>
<th>Random Effect</th>
<th>ID</th>
<th>Clutch</th>
<th>Trial Modality (Stationary, Moving, Acoustic)</th>
<th>Residual</th>
</tr>
</thead>
<tbody>
<tr>
<td>ID</td>
<td>25.176</td>
<td>-11.220</td>
<td>0.183</td>
<td>-7.705</td>
</tr>
<tr>
<td>Clutch</td>
<td>-11.220</td>
<td>9.9154</td>
<td>-0.120</td>
<td>0.165</td>
</tr>
<tr>
<td>Trial Modality (Stationary, Moving, Acoustic)</td>
<td>0.183</td>
<td>-0.120</td>
<td>1.428</td>
<td>-1.042</td>
</tr>
<tr>
<td>Residual</td>
<td>-7.705</td>
<td>0.165</td>
<td>-1.042</td>
<td>123.925</td>
</tr>
</tbody>
</table>
was negatively predicted by age, supporting the hypothesis that risk/novelty seeking increases with development/nutritional independence (Fig. 1). Trial class predicted approach, with novel objects being approached more frequently (Fig. 2). Individuals more socially dominant to their clutch-mates were more likely to approach stimuli (Fig. 3). Juveniles (mean age = 163 days) were more likely to approach than fledglings (mean age = 26 days) (Figs. 2 and 4), and the interaction between rank index and age class positively predicted approach frequency. This result may be confounded by the age-based hierarchy reported for this species (Zahavi, 1990). Juveniles were not tested at the same time as fledglings, but age variation within age classes (due to the presence of different clutch cohorts within age classes in some groups) and relative rank
within the group due to the presence or absence of older birds may have affected our results. For this reason, further research is necessary to parse apart the relationship between relative age and overall social rank with regard to novel stimulus approach. Juveniles of higher relative dominance over their own clutch-mates were the most likely birds to approach stimuli (Figs. 2 and 3). The presence of an adult at the beginning of recording also positively predicted approach frequency (Fig. 4), supporting a scrounger or observational learning context for novelty-seeking behaviours in this species, although as noted below, it is important to acknowledge that fledglings are rarely distant from adults due to nutritional dependence on parental provisioning (e.g. Ridley, 2007).

Our results shed light on a long-standing discussion of the relationship between social rank and neophilia, in which arguments have been made for both positive and negative correlations depending on ecological and social context (Boogert et al., 2006; Greenberg & Mettke-Hofmann, 2001). Unlike tests exploring this relationship through novel foraging behaviours, our study did not pair novel stimuli with food resources (Griffin, Lermite, Perea, & Guez, 2013). However, approaches to a novel stimulus in a familiar social context (the natal cooperatively breeding social group) were positively linked to the rank order of resource monopolization reported for Arabian babblers in that same context.

Table 5. Frequency of approach: predictor effects

<table>
<thead>
<tr>
<th>Fit Model</th>
<th>Least significant predictor</th>
<th>Effect size</th>
<th>SE</th>
<th>df</th>
<th>P</th>
<th>Wald statistic</th>
</tr>
</thead>
<tbody>
<tr>
<td>Full Model</td>
<td>Group size</td>
<td>-0.039</td>
<td>0.023</td>
<td>1</td>
<td>0.117</td>
<td></td>
</tr>
</tbody>
</table>
Table 6. Frequency of approach: fitted models

<table>
<thead>
<tr>
<th>Fit Model</th>
<th>Predictor removed to create model</th>
<th>r2 adjusted</th>
<th>RMSE</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Full Model</td>
<td>None</td>
<td>0.542</td>
<td>0.769</td>
<td>0.006</td>
</tr>
<tr>
<td>2</td>
<td>Group size</td>
<td>0.543</td>
<td>0.768</td>
<td>0.02</td>
</tr>
<tr>
<td>3</td>
<td>Order of presentation</td>
<td>0.544</td>
<td>0.768</td>
<td>0.007</td>
</tr>
<tr>
<td>Minimal Model</td>
<td>Sex ratio</td>
<td>0.544</td>
<td>0.767</td>
<td>0.0002</td>
</tr>
</tbody>
</table>

(Carlisle & Zahavi, 1986; Clutton-Brock & Harvey, 1976). Resource monopolization is fundamentally linked to intrabrood rank in many bird species (Drews, 1993), including Arabian babblers, which compete with siblings for resources by monopolizing space within the nest (Ostrieher, 1999), starting soon after hatching. Expressions and reinforcements of social rank among juveniles begin early in life and are often elicited by competition for food encountered during foraging (Carlisle & Zahavi, 1986; Zahavi, 1990).

While the similarity of babbler responses to the different stimulus modalities presented in this study (stationary object, moving object, acoustic stimulus) suggests a generalized response to novelty, tests using greater variation in stimuli than those presented here will further resolve this question. A wider range of objects featuring greater variation in size, colour/pattern, movement path and/or acoustic structure remains necessary to develop a more detailed
understanding of the relationship between novel object approach and risk taking. For example, none of the stimuli presented in this study were specifically intended to resemble high-risk stimuli (such as predators or dangerous anthropogenic items/sounds found near the habitat, including tractors or other machinery). Nor were the objects specifically designed to be associated with sources of food (for example, babblers may actively overturn sections of dried mud or inspect stationary plant material during foraging). In this way the neutral aspect of the stimuli permitted us to better access the inherent risk/reward question of novel object approach. Presenting a novel stationary plant, for example (different from the familiar leaves in the moving condition), might provide more detail on the specific foraging value of neophilic behaviour. Despite these limitations, we consider the finding of cross-modal preferential approach to neutral novel stimuli (as opposed to neutral familiar stimuli) to provide an important foundation for investigations into the relationship between formative social experience and ecologically relevant traits such as neophilia in more specific contexts.

Competitive experience and/or observation of socially dominant individuals may influence novel stimulus approach through a winner/loser effect (Frost et al., 2007). For example, blue-footed booby, Sula nebouxii, nestlings retain early life intrabrood rank even if the subordinate partner grows to outweigh the dominant partner, and they behave according to their role in the intrabrood hierarchy when confronted with novel dyadic partners (Drummond & Osorno, 1992). In turn, barnacle goose, Branta leucopsis, goslings experiencing early life success as subordinates (defined by a lack of aggressive response from siblings) are more likely to continue to attempt subordinate gestures in later interactions (Black & Owen, 1987).

Arabian babblers are known to engage in object-play in the form of ‘tug-of-war’ (Pozis-Francois, Zahavi, & Zahavi, 2004), from approximately 3 weeks after fledging. Novel objects
may evoke a similar monopolization attempt; in agreement, Arabian babblers have been characterized as inquisitive, and they initiate play behaviour by examining objects encountered during foraging and by choosing partners most similar in rank (Pozis-Francois et al., 2004). Social rank has been found to influence roles in wrestling and chase-based play, with dominant individuals taking the aggressive role and initiating play more frequently (Pozis-Francois et al., 2004).

If novel stimuli represent risks, early, frequent approaches may signal and communicate ability and contribute to (and be caused by) social prestige in babblers (Zahavi, 1995). As in the winner/loser effect paradigm, this may be both cause and effect. The presence of dominant individuals may inhibit the approach of subordinates (Drews, 1993; Soma & Hasegawa, 2004), and dominants may signal dominance by monopolizing resources, including opportunities to display quality to group members and eavesdroppers by assuming risk associated with novel stimuli (Zahavi, 1995). These paradigms are not mutually exclusive. If dominant individuals initiate object-based play through exploration of objects, as suggested by Pozis-Francois et al. (2004), novel stimuli may represent a high-risk/high-reward gamble. Monopolization may be preferable both as a display of condition through self-exposure to risk (Zahavi, 1995) and as an opportunity to control a potentially rewarding object or to play competitively. Stöwe et al. (2006) suggested that neophilia may explain why male ravens ‘show off’ in mixed-sex exposure trials. In our study, all groups were of mixed sex. Repeated winners in resource monopolization may be established among siblings from an early age (Carlisle & Zahavi, 1986); dominants may reinforce their dominance by relatively frequent and rapid approach to novel stimuli, and subordinates may reinforce their subordinate status by displaying behavioural inhibition.

Table 7. Covariance Matrix of Component Estimates: frequency of approach
<table>
<thead>
<tr>
<th>Random Effect</th>
<th>ID</th>
<th>Clutch</th>
<th>Trial Modality (Stationary, Moving, Acoustic)</th>
<th>Residual</th>
</tr>
</thead>
<tbody>
<tr>
<td>ID</td>
<td>0.000</td>
<td>0.000</td>
<td>7.638x10^-8</td>
<td>-2.482x10^-5</td>
</tr>
<tr>
<td>Clutch</td>
<td>0.000</td>
<td>0.001</td>
<td>-1.431x10^-7</td>
<td>5.413x10^-8</td>
</tr>
<tr>
<td>Trial Modality (Stationary, Moving, Acoustic)</td>
<td>7.6389x10^-8</td>
<td>-1.431x10^-7</td>
<td>8.511x10^-6</td>
<td>-2.348x10^-6</td>
</tr>
<tr>
<td>Residual</td>
<td>-2.482x10^-5</td>
<td>5.413x10^-8</td>
<td>-2.348x10^-6</td>
<td>0.000</td>
</tr>
</tbody>
</table>

Figure 2. Mean and + SE frequencies of approach separated by age class and trial class. Age class is divided between fledglings and juveniles. Trial class is separated between novel stimulus and familiar stimulus.

Since we did not collect data on daily body mass, it was not possible to determine the relative condition of each bird during testing. The context-dependent neophilia of individuals of low rank or poor condition may drive lower-ranking birds to engage in risky behaviour only after a threshold of hunger has been reached. This tactic may manifest as a blackmail tactic in the Arabian babbler's close relative, the pied babbler, *Turdoides bicolor* (Thompson et al., 2013):
birds in that study were fed bits of mealworm ad libitum at the beginning of each observation session. In contrast, in our study, since only small amounts were fed initially and trials did not begin until after normal foraging behaviour had resumed, individuals were unlikely to be satiated during trials.

Neophilic and risk-seeking behaviours have been consistently linked to juvenile or adolescent individuals (Greenberg & Mettke-Hofmann, 2001). Our results show that age class was the strongest predictor of approach speed, with developmental stage negatively predicting latency. Juvenile/adolescent individuals are physically mature (or nearly so), but they may be naïve relative to adults. Arabian babblers typically disperse later in life, beginning around 2 years of age (Zahavi, 1990), although in the present study, one female was subsequently observed to disperse at approximately 1 year of age. Arabian babbler young are more likely to engage in object-play behaviour than adults (Pozis-Francois et al., 2004), and dominance displays become more subtle and less aggressive in older babblers (Carlisle & Zahavi, 1986). Fledglings are more naïve relative to juveniles, and so may have experienced more noise in the environment that was novel versus familiar: experimentally presented novel objects may have been less attractive.
Figure 3. Mean frequencies of approach by rank index, separated by age class.
because many more objects in the environment are novel for younger individuals. Juveniles, with more experience and improved motor skills, may also simply be less vulnerable to the costs of risk taking, as well as being more mobile and independent of adults relative to fledglings (e.g. Ridley, 2007).

The finding that the presence of an adult babbler predicted more frequent approach, particularly in fledglings, allows for several nonmutually exclusive hypotheses. It may be that risk assessment influences novel stimulus investigation as well as observational learning. Subordinate adult Arabian babblers have been shown to act as scroungers more frequently than
dominants, although they are also better innovators of novel foraging strategies (Keynan et al., 2014). Although younger birds may be more neophilic or exploratory (see below), adult interaction with a novel stimulus may have a strong influence on young. Social learning, particularly between juveniles and adults, influences foraging and feeding behaviour in a wide variety of species (Lefebvre & Bouchard, 2003), and proximity to and observation of a conspecific influences novel object approach and exploration in several social bird species (Fritz & Kotrschal, 1999; Griffin & Boyce, 2009; Huber, Rechberger, & Taborsky, 2001; Langen, 1996; but see Griffin et al., 2013 on social inhibition of neophilic behaviour). The role of adult presence in facilitating approach demonstrates a decreased threshold of caution, which affects frequency of and latency to approach, and may support a risk-averse hypothesis, as the young may confirm the low-risk value of a novel stimulus through observation of an adult in proximity to the novel stimulus. If novelty is both risky and desirable, dominant young may be signalling and showing off (Zahavi, 1995) by exposing themselves to unknown risk (Stöwe et al., 2006). A confound in this interpretation is that fledglings (as compared to juveniles) are nutritionally dependent on adults (Ridley, 2007) and as a consequence are rarely distant from an adult. In a free-ranging population, it is unusual to observe fledglings in the absence of an adult.

The preference for novel over familiar stimuli, particularly among juvenile birds, combined with the apparent spatial monopolization of novel stimuli by higher-ranked individuals, strongly suggests that novel items are inherently attractive, supporting the risk-seeking hypothesis. Our finding that adult presence lowers the threshold for approach to novel stimuli also highlights the risk-taking aspect of approaching novel stimuli. We suggest that the frequent and relatively rapid novel object approach by dominant Arabian babblers may be a social tactic. Further research on context dependency (e.g. testing individuals in isolation) will be
necessary to support this argument, but approaches to novel stimuli (as a potential resource or danger) may reinforce rank and/or the presence of dominant individuals may inhibit neophilic approach behaviour by subordinate individuals in a priority-of-access model of hierarchy.

Acknowledgments

We are enormously grateful to Professors Amotz Zahavi and Avishag Kadman-Zahavi for advice and guidance. We also thank Oded Keynan, Yael and Gilad Alon, Arnon Dattner, and the Hazeva Field School and staff for their support. The research adhered to ASAB/ABS Guidelines for the Use of Animals in Research and the legal requirements of the State of Israel. The research was supported by a National Science Foundation Graduate Research Fellowship (issued to A. G. Fulmer: number 2012143588).

References


Behaviour, 141, 425-450.


Is autopreening a social signaling behavior in Arabian Babbler (*Turdoides squamiceps*) preening dyads?

Andrew G. Fulmer (corresponding author), Mark E. Hauber

Andrew Goldklank Fulmer: Animal Behavior and Comparative Psychology, Doctoral Program in Psychology, The Graduate Center, The City University of New York, 365 Fifth Avenue, New York, NY 10016-4309, USA

Mark E. Hauber: Department of Psychology, Hunter College and the Graduate Center, City University of New York, 695 Park Avenue, New York City, New York 10065, USA

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Running title: Autopreening in Arabian Babbler preening dyads

Word Count: 2988

*Correspondence: A.G. Fulmer, Dept. Psychology, Hunter College, 695 Park Avenue, New York, NY 10065, USA

E-mail: afulmer@gradcenter.cuny.edu

Telephone: +1(917) 734-5353
Abstract:

Allopreening/allogrooming is a conspicuous form of social interaction widely documented among animal lineages. In addition to the direct removal of ectoparasites or other detritus from plumage or pelage, for example, a social signaling function for these behaviors has also been strongly supported in several lineages. Participants (both actor and recipient) in preening/grooming dyads may encode a variety of information in the interaction, including hierarchical and affiliative information. The maintenance of hierarchy and reproductive skew is especially fundamental to the survival and fitness of cooperative breeders, which spend most of their lives in exclusive social groups making repeated interactional choices with the same individuals. Here we investigate the functions of allogrooming/allopreaming in the Arabian Babbler *Turdoides squamiceps*, a cooperatively breeding passerine; in particular, we focus on the role autopreening plays in the establishment of preening dyads. Using a database collected over a period of two years, we assess the interindividual relationship factors that predict the behavior of preening recipients following invitation to an allopreening bout by either the actor or the recipient. Relative age of individuals in preening dyads and the behavior of preening recipients prior to social approach significantly predicted the behavior of recipients following preening solicitation by actor and/or recipient. Specifically, actor age had a significant negative effect on the likelihood that recipients would autopreen before approaching the actor. When recipients invited preening by autopreening, they were significantly less likely to approach the actor. Recipients that did not conspicuously invite preening were significantly most likely to approach the actor without first autopreening. This evidence does not support the use of autopreening as a solicitous communication signal and instead it represents a visual display of displaced behavior, or an indicator of social indecisiveness.
Introduction:

Allogrooming and allopreening are social events in which one individual manipulates the fur or feathers of another (e.g. Wilkinson 1986; Radford & du Plessis 2006, Dunbar 2010). These behaviors are well documented as components of social tactics used by many species, though allogrooming has received more attention across mammalian systems than has allopreening in avian systems (e.g. Radford & du Plessis 2006; Schino 2007, Dunbar 2010). Both behaviors have been found to carry health benefits for the recipient as well as to serve as social signals (Lazaro-Perea et al. 2004, Radford & du Plessis 2006, Dunbar 2010). The social functions of grooming, including mediation of access to resources, tension reduction (Schino et al 1990), submission (Madden & Clutton-Brock 2009), dominance or competition (Harrison 1965; Zahavi 1995), social bonding (Seyfarth & Cheney 1984; Dooley & Judge 2007), and/or parental/alloparental interaction appear to be employed in different functional subsets among different species (Madden & Clutton-Brock 2009; Dunbar 2010).

Primates and some cooperatively breeding birds, including green woodhoopoes *Phoeniculus purpureus* (Radford & Du Plessis 2006; Dunbar 2010) and Arabian babblers *Turdoides squamiceps*, often groom/preen bodyparts of other individuals which those individuals could theoretically groom/preen themselves (Harrison 1965). Along with a number of observed social effects (e.g. Wey & Blumstein 2010; Dunbar 2010), this has been used as evidence that allogrooming has a function as social communication (Radford & Du Plessis 2006)

Allogrooming is often considered a fundamentally affiliative gesture (Dooley & Judge 2007; Wey & Blumstein 2010). For example, research on the role of allogrooming in social primates
and cooperatively breeding birds supports a tension-diffusing or alliance-building function (e.g. Radford & Du Plessis 2006, Dunbar 2010).

Displacement reactions/behaviors, or behaviors that are apparently unrelated to a given behavioral choice, have been a subject of interest since the foundation of ethology as a formal field of study (Tinbergen & Van Iersel 1946; Maestripieri et al. 2007). When individuals are presented with a behavioral choice involving an uncertain outcome, they may ‘take a third option’ by engaging in a behavior which commits them to neither of the original choices. This type of behavioral engagement may be particularly evident in situations where there is hierarchical or competitive ambiguity (Tinbergen & Van Iersel 1946; Van Iersel 1958). In this literature, then, autopreening, as well as other self-maintenance behaviors, are traditionally considered manifestations of stress in addition to their direct physical benefit, and are potential examples of a displacement behavior (Tinbergen & Van Iersel 1946).

Here we focused on the function of autopreening in the Arabian Babbler, which is a passerine that breeds cooperatively within closed and territorially-based social groups. These groups, typically 2-22 members in size, show high reproductive skew (Zahavi 1990; Anava et al. 2001). Groups typically include two socially and reproductively dominant individuals (a male and a female) and follow a linear dominance hierarchy strongly correlated with age. Older individuals are dominant to younger individuals, and males are typically dominant to females (e.g. Zahavi 1990; Kalishov et al. 2005).

Cooperative breeders typically live in small, exclusive groups in which individuals repeatedly interact over prolonged periods. The role of social touch in these taxonomically diverse species is of particular interest not only because of the prominence affiliative gestures play in exclusive, hierarchical groups but because the role of alloparents – the nonbreeding
helpers intrinsic to cooperative breeding – is itself the subject of a debate in which arguments (not necessarily mutually exclusive) are made both for direct health/fitness benefits to recipients of allopupal attention and for social signaling by allopups as driving selective factors (e.g. Zahavi 1995). Additionally, cooperative breeders often form groups based strongly around a set of parents and offspring. Not only do gestures typical of parent-infant interactions, including grooming, typify the interactions between parents and adult offspring in this core group, these behaviors also occur between retained offspring and non-descendant litters or clutches. In the Arabian Babblers, immigrant and unrelated allopups also act with parental gestures towards younger members of the group (Zahavi 1990; Kalishov et al. 2005). It may therefore be expected that the functions of allopuping networks will take on a discrete functional role in Arabian Babblers.

We attempt to distinguish between two possible explanations for instances where autopuping occurs on its own and instances in which it takes part in the sequence of events immediately prior to formation of a preening dyad. One hypothesis is that autopuping is fundamentally communicative: an indication of need. We suggest that in the communicative solicitation hypothesis, closely bonded individuals, or individuals seeking to increase a bond, will autopup to prompt or solicit preening. We also propose an alternative hypothesis: that autopuping may function as a displacement behavior. In this scenario we expect to find increased autopuping when bonds between allopuping partners are ambiguous or uncertain. The formation of an allopuping dyad, as described in this study, can be broken down into three components: invitation, behavior following invitation (approach style) and allopuping event. Here we focus on the role of autopuping in the invitation style and behavior following invitation (approach style).
Methods:

Study Site and Animals:

All data were collected from free-ranging individuals on the Shezaf Nature Reserve in the Negev desert near Hazeva, Israel, 30°48’N 35°13E’ (sensu Keynan et al. 2014). The reserve is an arid desert with varied savannah and sandy terrain, having a mean annual rainfall of 35mm (Anava et al. 2000; Keynan et al. 2014). Wadis (river beds which are dry almost year-round, but may briefly flood during the rainy season) and dunes are significant topographical features; acacia trees (Acacia tortilis, A. radiana) are the major flora and often serve as the nesting site of Arabian Babbler groups (Zahavi 1990; Anava et al. 2000; Keynan et al. 2014). Data used in this analysis were collected by Arnon Dattner, Carmel Zener, and Professors Amotz Zahavi and Avishag Kadman-Zahavi from 29 December 2002 – 30 April 2004, including breeding and non-breeding seasons. Observations occurred in morning (~sunrise), midday, and evening (~sunset). A total of 38 Arabian Babblers were included in this analysis, following the implementation of several exclusion criteria. Only interactions where the initiator of contact between the two individuals and the identity of both individuals was known were included in the analysis. Of these interactions we used only those including adults (approximately less than 1 year of age) or juveniles (approximately less than 3 months of age), where the sexes of both individuals were known. The population studied was banded, habituated to observer presence, and censused regularly as part of an ongoing study (since 1971) by Professors Amotz Zahavi and Avishag Kadman-Zahavi (Zahavi 1990; Keynan et al. 2014). With the exception of individuals that appeared at the study site as adults, all birds were banded at approximately 8 days of age, and habituated with the presentation of mealworms and/or bread in the presence of observers. All
sufficiently habituated observed individuals were satiated (defined at the point where they no longer approached mealworms, bread, or water) before each observation session, to control for condition. Rank was tested by the standard practice of the Arabian Babbler Research Project (a form of scramble competition) (see Carlisle & Zahavi 1986). All work adhered to the guidelines for the use of animals in research, as published in Animal Behaviour (1991), as well as the relevant laws and regulations of Israel.

**Data Analysis:**

A database tabulating all observed dyadic preening interactions was used for this analysis (please see methods for exclusion criteria). The initiator of contact was defined as the actor in the preening dyad, while the individual with which contact was made was defined as the recipient. Behavior associated with social approach or lack of approach to actors, by recipients, was termed “recipient behavior following invitation to preen/be preened.” This behavioral category was used as the predicted variable, and included instances where individuals were observed to autopreen, then approach the actor, approach without autopreening, or not approach at all. No approach was used as the reference group for pairwise comparison with both approach styles.

The relative age classes of the actor and recipient defined the predictor variable “age dyad.” “Older actor” referred to adult actor/juvenile recipient dyads. “Same age class” included both adult actor/adult recipient and juvenile actor/juvenile recipient dyads. “Younger actor” referred to juvenile actor/adult recipient dyads. Behavior of either actor or recipient immediately prior to the approach of one individual to another before initiation of the preening event was termed “invitation style.”
A backwards elimination procedure (Grafen & Hails 2002) was used on a multinomial logistic regression model. A full model using these six predictor variables was first generated. We then removed the least significant predictor from each model (p > .05), resulting in a minimal model including only statistically significant predictors (Table 1). The association between the recipient behavior following invitation to preen/be preened and the remaining predictors in the two pairwise tests was tested using chi-squared tests. Analyses were performed in SAS/JMP 12 statistical software™.

**Results:**

**Recipient behavior following invitation to preen/be preened:** Age dyad, breeding status dyad, intrasex rank dyad, sex dyad, actor invitation style, and recipient invitation style were used as predictor variables before the onset of the step-wise elimination procedure. The full model is shown in Table 1.

**Table 1. Fit models of recipient behavior following invitation to preen/be preened.**

<table>
<thead>
<tr>
<th>Fit Model</th>
<th>Least significant predictor(s)</th>
<th>Nparm</th>
<th>df</th>
<th>Wald $X^2$</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Full Model</td>
<td>Breeding status dyad</td>
<td>2</td>
<td>2</td>
<td>2.809</td>
<td>0.245</td>
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<tr>
<td>2nd Model</td>
<td>Intrasex rank dyad</td>
<td>4</td>
<td>4</td>
<td>3.950</td>
<td>0.412</td>
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<tr>
<td>3rd Model</td>
<td>Sex dyad</td>
<td>6</td>
<td>6</td>
<td>10.086</td>
<td>0.121</td>
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<tr>
<td>4th Model</td>
<td>Actor invitation style</td>
<td>4</td>
<td>4</td>
<td>7.563</td>
<td>0.108</td>
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<tr>
<td>Minimal Model</td>
<td>Age dyad</td>
<td>4</td>
<td>4</td>
<td>17.743</td>
<td>0.001*</td>
</tr>
</tbody>
</table>
Age dyad type significantly predicted recipient behavior following the invitation (Table 1). When actors in a preening dyad were older than recipients (adults preening juveniles), the recipient was the only factor remaining as significant; specifically, the recipients were most likely to approach without autopreening (Est. 1.505, SE ± 0.44, $X^2 = 11.69$, $p = 0.0006^*$) (Fig. 1).

Fig. 1 Total count + SE frequency of recipient behavior following invitation to preen/be preened by age dyad type

Recipient invitation style was defined as the behavior engaged in by the recipient of contact prior to a preening bout. This significantly predicted the next behavior engaged in by the recipient
(which by definition of recipient could not include making preening contact with the actor) (Table 1). Specifically, when recipients invited preening by autopreening, the recipient was significantly most likely to respond with no approach to the actor (Est. -3.018, SE ± 0.516, X² = 34.20, p = 0.0001*). When recipients did not conspicuously invite preening, they were significantly most likely to approach without first autopreening (Est. 2.917, SE ± 0.591, X² = 24.30, p = 0.0001*) (Fig. 2).

![Graph showing recipient behavior following invitation to preen/be preened](image)

Fig. 2 Total count + SE frequency of observed recipient behaviors following invitation to preen/be preened for each recipient invitation style.

**Discussion:**
We found evidence that the style of approach by the recipient in an allopreaming dyad is reflective of the interindividual relationship between actor and recipient, and, more specifically, that autopreening functioned as a displacement behavior when the relationship was ambiguous. Autopreening is often considered a stress-related behavior associated with displacement of tension (Maestripieri 2007; Wascher et al. 2010). As a self-directed behavior, it may function as a signal of hierarchical or social bond related uncertainty without exacerbating tension through contact with the other individual.

**Age dyad**

Approach without a delay in the form of autopreening was most frequent when older birds were the actor (adult-juvenile dyads) (Fig. 1). Age is strongly and positively correlated with dominance within Arabian babbler groups (Zahavi 1990) and so it is likely recipients were responding quickly to unambiguously dominant individuals. Since age classes could contain multiple age cohorts, same-age actor and recipient dyads could also contain older/younger recipients, though these individuals were at the same developmental stage. Older actor and younger actor dyads were by definition unambiguous in containing individuals from different cohorts. Allogrooming has been shown to be directed down the age-linked hierarchy in other cooperative breeders, such as the yellow-bellied marmot (Wey & Blumstein 2010).

Arabian babblers exhibit a producer-scrounger foraging system, in which subordinate (though not necessarily chronologically younger) birds behave as scroungers, following dominant birds and apparently observing novel foraging techniques, as well as benefitting from successful location of food sources, including potentially novel food types or novel objects in the terrain, by dominants (Keynan et al. 2014). Juveniles, particularly juveniles dominant to their
clutchmates, show neophilic behavior when approaching inanimate stimuli (Fulmer et al. 2016) and so may also be socially neophilic. Juveniles are not nutritionally dependent upon adults (as fledglings are) (Ridley 2007) but still receive allofeeding or may benefit through observational learning (Kalishov et al. 2005; Ridley 2007; Keynan et al. 2014). Therefore, a juvenile would have a stronger, unambiguous motivation to increase social bonds with older, more dominant and/or experienced, individuals. Allopreening has often been described as a tactic for cementing social bonds (Dooley & Judge 2007, Dunbar 2010). These relationships are socially certain. They include an actor much more likely to be dominant to the recipient (Zahavi, 1990) and more likely to provide nutritional or cognitive benefits (Ridley 2007; Keynan et al. 2014). Conspicuous display of hesitation (by autopreening) may not benefit juvenile members of adult-juvenile dyads under these circumstances.

**Recipient invitations**

That recipient invitation style predicted the following behavior (approach style) of the recipient is not surprising, and supported the hypothesis that pre-preening activity has signaling value. Recipients were significantly less likely to approach actors after autopreening, further supporting the displacement behavior hypothesis for autopreening. If autopreening functions as a signal of hierarchical uncertainty, we expect that it will be more frequent when recipients in allopreening dyads have less social compulsion to respond to actors. There is also evidence that autopreening may function as a component of tense interactions, rather than a mechanism for reducing tension, as in Graylag geese, where it is associated with greater duration of elevated heart rate following agonistic encounters (Wascher et al. 2010).
The absence of autopreening before allopreening contact in more socially certain situations, and its presence in potentially uncertain situations, strongly suggests that in the context of establishing allopreening dyads, autopreening is a socially mediated displacement behavior. Among Arabian Babbler groups, reproductive opportunity is tied to social dominance and social dominance is, in turn, linearly associated with increased age (Zahavi 1990). Given the opportunity to engage in allopreening dyads with older individuals, younger Arabian babblers were unlikely to display indecision; we found that autopreening was not likely to occur when older individuals function as the allopreening actor. When recipients of preening have not given an indication of inviting, or soliciting, the preening event, they were similarly likely to approach without first autopreening. If the individual approached but did not make a solicitous gesture, it follows that another aspect of the social context compelled that individual to engage in the preening dyad without hesitation. Further analysis of the role of actor invitation and ontogenetic/experiential aspects of both individuals here is necessary to pinpoint this aspect.

Finally, when recipients employed autopreening as a component of the invitation/solicitation for a preening event, they were significantly less likely to approach the actor. This finding further supports that autopreening may indicate a lack of certainty about the value of engaging in the preening dyad, or at least about acting as the recipient in that particular dyad. A displacement behavior may have multiple functions, including self-soothing and communication of distress or social uncertainty (Maestripieri 2007). Further research on the sequence of events in the establishment of preening dyads in which autopreening behavior occurs, including longitudinal study of the interactions following the event and the forcefulness of the event, will help to clarify its social significance.
Acknowledgements: We are particularly grateful to Arnon Dattner for designing the research presented here and leading the data collection effort, as well as generously making available the data for future analysis and interpretation. We also thank Carmel Zener and Professors Amotz Zahavi and Avishag Kadman-Zahavi for developing this research, collecting data, and providing advice, and Oded Keynan, Roni Ostreicher, and Yael and Gilad Alon for support and advice. Data analysis and interpretation was supported by a National Science Foundation Graduate Research Fellowship (issued to A.G. Fulmer: number 2012143588).

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Social plasticity in non-territorial male African cichlid fish *Astatotilapia burtoni*

A.G. Fulmer\(^1\)*, H. Neumeister\(^2\), T. Preuss\(^2\)

\(^1\)Animal Behavior and Comparative Psychology, the Graduate Center of The City University of New York, NY, USA

\(^2\)Department of Psychology, Hunter College, City University of New York, NY, USA

Running Headline: Behavioral plasticity of *Astatotilapia burtoni* males

Tables: 1

Figures: 7

Total text pages: 18

*corresponding author: Andrew G. Fulmer; Training Area in Animal Behavior and Comparative Psychology, Graduate Center of The City University of New York, 365 Fifth Avenue, New York, NY 10016-4309, USA; Tel: +1 917 734 5353; afulmer@gradcenter.cuny.edu.
ABSTRACT

The African cichlid fish *Astatotilapia burtoni* represents a valuable model system for studies of social decision making due to its socially mediated phenotypic plasticity. Males reversibly transition in social status from reproductively dominant and territorial (DOM) to submissive and non-territorial (SUB). Males are traditionally categorized into these two behavioral phenotypes by observational scoring. There is evidence, however, that this dichotomous categorization might not capture the behavioral plasticity displayed by individuals transitioning between SUB and DOM status. To test this concept, we used focal observations of intrasexual conflict behavior in fish communities combined with a modified analysis of the ethogram typically used in *A. burtoni*. Results revealed a cluster of males close to the crossover point between SUB and DOM status as defined by the traditional Dominance Index. These intermediate males (INT) showed the highest frequency of intrasexual conflict behaviors, distinct behavioral responses to threats, and body pigment signaling displays that distinguish them from prototypical SUBs and DOMs. As such, our results provide a noninvasive behavioral metric to categorize *A. burtoni* males into three groups, thus further capturing the complex social dynamic of this model organism.

Key words: Social behavior. Reversible phenotype. Dominance. Territoriality. Intrasexual competition.
INTRODUCTION

Competition for resources, including mating opportunities, shelter, and food access, has a strong influence on many experiential and fitness related/life history traits of individuals in a social system (e.g. Erickson 1967; Genner et al. 1999; Maher and Lott 2000; Clement et al. 2005). Variation based on success in these competitions is often used to characterize individuals in terms of community hierarchy, territory ownership, reproductive opportunity, and cooperative contributions (e.g., Baerends and Baerends-Van Roon 1950; Rowland 1997; Hofmann et al. 1999; Oliveira et al. 2002; Chen and Fernald 2011). These characteristics, as well as traits such as sex, age, and reproductive status contribute to determining social status and often are used as a comparative baseline in research on many aspects of social behavior in many taxa (e.g. Dittus 1977; Ågren 1984; Stutchbury 1994; Hofmann et al. 1999; Clement et al. 2005; Chen and Fernald 2011).

The African cichlid fish *Astatotilapia burtoni* (Günther 1894) represents a well-characterized vertebrate model system for examining the effects of the social environment on behavior (as well as physiology), as males reversibly switch phenotype in strong association with social cues (e.g. Fernald 1977; Greenwood and Fernald 2004; Burmeister et al. 2005; Clement et al. 2005; Renn et al. 2009). Males transition in social status from being territorial (DOM) and monopolizing reproduction to being non-territorial (SUB) without functional gonads, and vice versa (e.g. Fernald 1977; Renn et al. 2009). In a social community, *A. burtoni* congregate around a lek-like set of territories. The territories are occupied by DOMs while SUB males and females spend the majority of their time shoaling together (Fernald 1977; Fernald and Hirata 1977; Ferno 1987; Korzan et al. 2008; Renn et al. 2009).
Traditionally, a Dominance Index (DI) score is calculated for individual *A. burtoni* to characterize social status (Korzan et al. 2008; Renn et al. 2009). Specifically, agonistic, territorial, and reproductive behaviors are added and scored as positive values. Submissive behaviors such as fleeing are scored as negative values. The total combined value is used to calculate the DI. Due to the nature of the behaviors scored, the DI inherently reflects the outcome of agonistic encounters: submissive behaviors reflect a losing outcome for the individual by definition. To the best of the authors’ knowledge, this index is currently the only noninvasive metric used to characterize male types in this species. The DI divides males by classifying them either as DOM (positive value) or SUB (negative value) with a DI of zero used as the crossover or point of division between these two groups. However, there is evidence that this dichotomy might not capture the behavioral and physiological plasticity displayed when it comes to individuals transitioning between SUB and DOM status (Fernald 1977; Fernald and Hirata 1977; Hofmann et al. 1999; Desjardins et al. 2012). Some individuals which do not show the traits of full DOMs still do exhibit a more DOM-like hormonal suite as compared to SUBs, and observation in the wild showed that some SUBs and not-fully-DOM individuals, also engage in conflicts that do not result either in fleeing or aggressive response (Fernald and Hirata 1977; Hofmann et al. 1999). Additionally, males ascending to DOM status appear to monitor aggression among other males, with attention directed up the hierarchy (Desjardins et al. 2012).

In sum, the physiological and behavioral traits exhibited by transitioning males suggests that the social pressures associated with ascent to or descent from DOM status are possibly distinct enough to be considered as an additional male phenotype (Hofmann et al., 1999; Oliveira et al., 2002; Korzan et al., 2008). Thus, we predict that males of uncertain territorial status (i.e. near zero DI score) are likely to behave not only more similarly to one another as compared to
either prototypical, fully established DOMs or to prototypical, fully submissive SUBs, but also
with a distinct behavioral suite more reflective of a greater potential range of outcomes to
introsexual conflict. Our results show that a modified version of the traditional DI ethogram, and
an alternative quantification, the “conflict index” (CI), can be used for a noninvasive
categorization of such a third male phenotype within *A. burtoni* communities.

**MATERIALS AND METHODS**

**Subjects**

Two communities, each containing 10-12 male and 5 female lab strain *A. burtoni* were used for
behavioral observations. Individuals were originally obtained from the Hofmann lab at the
University of Texas, Austin, but have been bred in the Preuss lab for several generations. They
were housed in acrylic tanks (30x30x60 cm) with flow-through conditioned water maintained at
pH 8.5 ±0.2; 27 ±0.2 °C; 550-650 µS/cm conductivity to ensure a constant environment
appropriate to *A. burtoni*. Terra-cotta pots were provided to permit males to form territories.
Cichlids were fed daily using a standard aquarium cichlid diet. The room was kept on a 12-hour
light/dark cycle. These conditions, specifically tank size, population density, and subject strains
are standard in research on *A. burtoni* social plasticity (e.g. Hofmann et al. 1999). Although the
body lengths of individuals used in this study were not measured (see rationale below) other
studies in our laboratory show that the standard body length of experimental males from the
laboratory population typically ranges between 5.5 and 8 cm. Tank size and number of animals
per tank were chosen to match previous studies in *A. burtoni* (e.g. Neumeister et al. 2010). Each tank typically contained 3-5 established territories.

**Behavioral focal observation**

Ethogram recordings were taken using a continuous sampling method according to previous categorization of male social status in this species (Baerends and Baerends-Von Roon 1950; Fernald 1977; Burmeister et al. 2005; Fox et al. 1997; Renn et al. 2009). Each male was observed as a focal animal for 10 minutes twice weekly between 10:00 and 14:00 for a total of sixteen observations. Before each initial observation within a session, a 10-minute period was allowed to acclimate the fish to the presence of the observer. Communities were assembled and undisturbed for weeks, without focal observation, prior to this experiment. To minimize interference with the behavior of individuals and the development of the social system, body size, gonadal growth and hormonal status were not recorded. The existing ethogram was modified to accommodate additional categorization as explained below (additionally, see Table 1). Prior to the experiment, individuals were superficially marked for identification using small patterns applied with Alcian Blue 8GX dye. Although males engaged in physical confrontations, no serious injury was observed during the study. All procedures were conducted according to the guidelines of the Hunter College CUNY IACUC.

**Table 1**

<table>
<thead>
<tr>
<th>Behavior</th>
<th>Definition</th>
<th>Mean, SD by Male Phenotype (DOM=Highest DI, INT=Intermediate DI, SUB=Lowest DI)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Confrontations</strong></td>
<td>Includes all agonistic encounters including flee, excludes shoaling and pigment displays</td>
<td></td>
</tr>
<tr>
<td>-------------------</td>
<td>----------------------------------------------------------------------------------</td>
<td></td>
</tr>
<tr>
<td><strong>Threats</strong></td>
<td>Includes all aggressive behaviors initiated by the focal fish, excludes flee, ignore threat, shoaling and pigment displays</td>
<td></td>
</tr>
<tr>
<td><strong>Reproductive</strong></td>
<td>Spawning, nest-building, and courtship</td>
<td></td>
</tr>
</tbody>
</table>

**Behaviors**

<table>
<thead>
<tr>
<th><strong>Behavior</strong></th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bite (+)</td>
<td>Physical contact with mouth closing on other individual</td>
</tr>
<tr>
<td>Poke (+)</td>
<td>Physical contact, not resulting in bite</td>
</tr>
<tr>
<td>Chase (+)</td>
<td>Shortening distance to target abruptly, independent of target reaction</td>
</tr>
<tr>
<td>Threat Display (+)</td>
<td>Back-and-forth movement often accompanied by opercular flaring, typically oriented towards other males</td>
</tr>
<tr>
<td>Border Threat (+)</td>
<td>Same as threat display but occurs at the border of territory, or “scrape”</td>
</tr>
<tr>
<td>Carousel (+)</td>
<td>Dyadic circular movement of opponents with each individual shortening distance to opponent's tail</td>
</tr>
</tbody>
</table>

**Ignore threat**

Threatened individual does not respond with freezing, flight or other displacement, and remains swimming/ floating without response visible to observer

**Flee (-)**

Increasing distance abruptly as response to chase or poke

**Shoal**

In close proximity with two or more conspecifics (typically 1-2 body lengths)

<table>
<thead>
<tr>
<th><strong>Lachrymal stripe display</strong></th>
<th>Melanistic pigment, vertical black stripe on either side of the head in lachrymal area (Desjardins and Fernald, 2008)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Vertical stripe display</strong></td>
<td>Melanistic pigment, on either side of the body along rib area (Fernald and Hirata, 1979)</td>
</tr>
</tbody>
</table>

**All threats:**

<table>
<thead>
<tr>
<th>Category</th>
<th>Mean ± SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>DOM</td>
<td>48.66 ± 9.88</td>
</tr>
<tr>
<td>INT</td>
<td>39.36 ± 5.09</td>
</tr>
<tr>
<td>SUB</td>
<td>1.09 ± 0.78</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th><strong>Ignore threat:</strong></th>
</tr>
</thead>
<tbody>
<tr>
<td>DOM: mean 1.88 ± 2.31</td>
</tr>
<tr>
<td>INT: mean 9.25 ± 1.49</td>
</tr>
<tr>
<td>SUB: mean 0.49 ± 0.33</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th><strong>Flee:</strong></th>
</tr>
</thead>
<tbody>
<tr>
<td>DOM: mean 3.80 ± 6.52</td>
</tr>
<tr>
<td>INT: mean 35.61 ± 3.80</td>
</tr>
<tr>
<td>SUB: mean 21.83 ± 10.49</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th><strong>Shoal:</strong></th>
</tr>
</thead>
<tbody>
<tr>
<td>DOM: mean 8.97 ± 15.40</td>
</tr>
<tr>
<td>INT: mean 75.44 ± 4.38</td>
</tr>
<tr>
<td>SUB: mean 96.75 ± 2.38</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th><strong>Lachrymal stripe display:</strong></th>
</tr>
</thead>
<tbody>
<tr>
<td>DOM: mean 94.46 ± 11.03</td>
</tr>
<tr>
<td>INT: mean 50 ± 5.25</td>
</tr>
<tr>
<td>SUB: mean 3.16 ± 4.15</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th><strong>Vertical stripe display:</strong></th>
</tr>
</thead>
<tbody>
<tr>
<td>DOM: mean 39.95 ± 13.78</td>
</tr>
<tr>
<td>INT: mean 73.61 ± 12.52</td>
</tr>
<tr>
<td>SUB: mean 21.48 ± 24.95</td>
</tr>
</tbody>
</table>
**Dominance and Conflict Indices**

During each focal observation session, the Dominance Index (DI) was calculated by subtracting the number of (-) submissive behaviors i.e. fleeing, from the number of (+) dominant behaviors i.e. threats, reproductive behaviors, exhibited by a given male (Table 1) (Fernald 1977; Fox et al. 1997). The mean DI score of each male was then calculated from the individual session DI scores throughout the eight-week observation period. To test for grouping patterns within the arrays of behaviors salient to territorial status (N=22) we applied agglomerative hierarchal cluster analyses using the Ward’s minimum variance method (JMP Pro 11). For validation, behavioral patterns between the clusters were compared with one-way ANOVA followed by Tukey posthoc tests when appropriate, and with simple linear regressions (JMP Pro 11).

We also developed an alternative analysis of the above ethogram that highlights the overall number of intrasexual agonistic encounters of males: Conflict Index (CI). The CI is the sum (rather than the difference) of submissive and threat behaviors, both having positive (+) value, and excludes reproductive behaviors (see results for rationale).

**RESULTS**

**Behavioral phenotypes in *A. burtoni***

To identify possible behavioral subtypes within *A. burtoni* communities we applied a combined cluster analysis that used three behavioral variables related to territorial status: threat, flee, and shoal. Figure 1a presents a dendrogram of the clustering sequence of 22 males that suggests a...
three cluster division as the most parsimonious, as indicated by the distance scree plot (Fig. 1b). Specifically, intracluster homogeneity (the similarity of scores within a cluster) and intercluster heterogeneity (difference between of scores among clusters) are maximized by a three cluster solution as indicated by a sharp rise in data variance following the third segment in the scree plot (vertical line Fig. 1b).

The mean DI scores of males in these three clusters exhibited considerable range, which reflects the behavioral dynamic and social plasticity in *A. burtoni* communities (Fig. 1a). Importantly, the three clusters do not follow strictly the (-) and (+) DI score dichotomy (Fig. 1a). Namely, the clusters subdivided males with clearly (+) DIs (mean DI 45.44±SD 14.09; N=7) and those with clearly (-) DIs (mean DI -21.04±SD 9.99; N=8). However, the analysis also suggested an intermediate (INT) cluster of males with DI scores near zero (mean DI 3.78±SD 5.17; N=7), based on threat, flee, and shoal behaviors (Fig. 1a). This triadic split was supported by a one-way ANOVA, F (2,21)=77.25, p<0.0001 and subsequent posthoc tests that revealed significant differences between all three clusters (Fig. 1c).
Fig. 1

(a) Distance scale dendrogram of a hierarchical cluster analysis based on the behavioral variables threat, flee, and shoaling for each male (N=22) using the Ward linkage method. The mean DI score for each of the individual males is indicated (left column). (b) Scree plot showing the distance bridged to join clusters at each step. Solid vertical line indicates the parsimonious break point where distance increases abruptly, suggesting three cluster groups. (c) Box plots showing the DI values for DOM, INT and SUB males. The horizontal line within the box represents the median sample value. Brackets represent post hoc (Tukey) comparisons between the three male cluster groups (****<0.0001); (**=0.0005).
Figure 2 shows a detailed timeline of each male’s social trajectory over the entire observation period including the number of social transitions with respect to the DI score. The results highlight the transitional status of males in the INT cluster and the social uncertainty faced by this phenotype (Fig. 2b). This interpretation is supported by the number of zero DI crossover point transitions made by males in each of the clusters over the course of the observational period (Fig. 2). Six out of seven individuals belonging to the INT cluster made a transition during the observation period. Five of them transitioned more than once (Fig. 2b). In contrast, only one individual belonging to the DOM cluster transitioned, while other DOMs consistently had positive DI scores (Fig. 2a). Similar to the DOMs, only one individual belonging to the SUB cluster made a transition, while other SUBs remained negative DI scores (Fig. 2c).
Timeline plots showing the weekly average DI for each male (see color code to the right for individual IDs) belonging to the (a) high DI cluster (DOM), (b) the intermediate DI cluster (INT), and (c) the low DI cluster (SUB). Dashed lines indicate the zero DI crossover point for social transitions.

Fig. 2
Together, the results suggest that males with clearly negative DI scores exhibited behaviors and a (subjectively assessed) gross phenotype typical of fully submissive, non-reproductive individuals (prototypical SUB males) and those with clearly positive DI scores exhibited behaviors and a (subjectively assessed) gross phenotype typical of fully territorial and reproductive individuals (prototypical DOM males). However, the phenotype of INT males, i.e., low positive or low negative DI scores is not readily apparent.

In principle, a DI score close to zero can reflect either the sum of a sizable but similar number of dominant (+) and submissive (-) behaviors, or alternatively, an overall low frequency of social interactions per se. In other words, the DI does not clearly distinguish between active and passive individuals close to the crossover point. In this way, potentially important information about the individual frequency of intrasexual conflict behaviors that regulate phenotypic plasticity in the species may be overlooked.

To resolve this ambiguity, we developed the Conflict index, CI (see Methods). CI differed significantly within the three clusters (F (2,21)=73.76, p<0.0001; one-way ANOVA). INT males showed the highest CI (mean 84.23±SD 8.34), followed by prototypical DOMs (mean 54.35±SD 9.22) and prototypical SUBs (mean 23.42±SD 11.03), respectively (Fig. 3).
Fig. 3
Differences in conflict index (CI) between cluster groups. Box plots showing the distribution of CI values for DOM, INT, and SUB males. The horizontal line within the box represents the median sample value. Brackets represent post hoc (Tukey) comparisons between the three male groups (****<0.0001)
We next asked if INT cluster males exhibit other behaviors that distinguish them from prototypical SUB and DOM males. To explore the latter notion, we analyzed the frequency of behaviors typically not part of the DI ethogram yet readily observable during agonistic interactions. Indeed, INT males responded to threats either with returned threat, fleeing, or by failing to be displaced: a behavior named here ‘ignore threat’ (see Table 1; see also Fernald and Hirata 1977). This behavior differed significantly among the clusters (F (2,21)=65.68, p<0.0001; one-way ANOVA) and, intriguingly, was shown almost exclusively by INT males (Table 1, Fig. 4a). Ignore threat behavior is also positively correlated to CI (r^2(21)=0.75; p<0.0001) (Fig. 4b). The latter result suggests that males that ignore threats are highly active. Our results, however, show that these males are not the ones that also deliver threats most frequently (Fig. 4c). Indeed, the results imply that prototypical DOMs most frequently perform threats, with INT and prototypical SUB males showing intermediate and close to zero threat frequencies, respectively (Fig. 4c). No consistent temporal pattern in the display of this behavior was found in the observations presented here.
Differences in frequency of the agonistic behavior ‘ignore threat’ between the three male mean cluster groups. (a) Box plots showing the distribution ‘ignore threat’ for DOM, INT and SUB males. The horizontal line within the box represents the median sample value. Brackets represent post hoc (Tukey) comparisons between the three groups (***, p<0.0001). (b) Linear regression between individual CI scores and ‘ignore threat’ behavior for all males in the three groups (***p<0.0001; N=22; r^2=0.75). Shaded area indicates 95% confidence limits. (c) Heat map of the mean total 'threat' by the mean total 'ignore threat' per individual indicating the three male cluster groups.

**Phenotypic pigment displays**

Lateral body pigment displays are used by A. burtoni males for social signaling (e.g. Baerends and Baerends-Von Roon 1950; Desjardins et al. 2012) and thus might also provide a marker for identifying INT males. The lachrymal stripe display is associated with territorial dominance in A. burtoni (Fernald and Hirata 1979; Desjardins et al. 2012). Accordingly, the results showed that the frequency of this display significantly differed within the clusters (F (2,21)=291.43, p<0.0001; one-way ANOVA). Prototypical DOMs displayed lachrymal stripes with greatest frequency, followed by INT males and prototypical SUBs, respectively (Table 1, Fig. 5a). A weak yet significant correlation existed between lachrymal stripe display and CI (r^2(21)=0.26; p=0.01) (Fig. 5b).
Another socially mediated reversible pigment display, the vertical stripe display, appears during male-male conflicts and is typically quantified as percent display time during focal observation (Fernald and Hirata 1979) (Table 1). Comparing the frequency of vertical stripe display revealed significant differences among the DI cluster cohorts (F (2,21)=15.20, p<0.0001), which was driven by a high frequency of occurrence in INT males (Table 1, Fig. 6a).
The data also yielded a significant positive correlation between vertical stripe display and CI 
\( r^2(21)=0.70; p<0.0001 \) (Fig. 6b).

Fig. 6
Differences of vertical stripe display between the three male groups. (a) Box plots showing the 
distribution for stripe display [% time] for DOM, INT and SUB males. The horizontal line within 
the box represents the median sample value. Brackets represent post hoc (Tukey) comparisons 
between the three male groups (**** \( \leq 0.0001 \); **=0.007). (b) Linear regression between 
individual CI scores and vertical stripe display for all males in the three groups (p<0.0001; N=2; 
\( r^2=0.70 \)). Shaded area indicates 95% confidence limits.

Summary cluster analysis
Finally, to further substantiate and validate the division of males into three groups we expanded our original cluster analysis to include the behavioral variables discussed above (i.e. an analysis based on threat, flee, shoal, ignore threat, lachrymal stripe display, and vertical stripe display). Figure 7 shows the clustering sequence and distance scree plot of the 22 males indicating that intracluster homogeneity and intercluster heterogeneity are maximized by a three-cluster solution. Importantly, all individual males remain in the original cluster into which they were sorted previously (see Fig. 2 for fish IDs).
Fig. 7

(a) Distance scale dendrogram of a hierarchical cluster analysis of all behavior variables described in this study (threat, flee, shoal, ignore threat, lachrymal stripe display, and vertical stripe display) for each individual male (N=22) using the Ward linkage method. (b) Scree plot showing the distance bridged to join clusters at each step. Solid line indicates the parsimonious break point where distance increases abruptly, suggesting three clusters.
DISCUSSION

The goal of this study was to develop a non-invasive method to further categorize *A. burtoni* males. Specifically, we focused on males that are close to the crossover point between SUB and DOM status as defined by the traditional DI. These INT males showed the highest frequency of intrasexual conflict behaviors i.e., the highest CI scores. In addition, at least two distinct male-male conflict-related characteristics, the ignore threat behavior and expression of the vertical stripe display, further distinguish these INT males from prototypical SUBs and DOMs. Results suggest that a combined analysis of an extended DI ethogram and CI scores can reliably identify a unique behavioral suite for a distinct group of males in *A burtoni*.

Our analysis using the traditional DI ethogram, along with an alternative quantification of intrasexual conflict behavior, permits a more nuanced classification of the INT males as a distinct phenotype. These analyses contribute to a better understanding of the relationships between social status and risk avoiding and/or aggression-reducing strategies that are currently being studied in many taxa (e.g. Judge and De Waal 1993; Harris et al. 2010; Černá et al. 2013). The finding that males in more variable social circumstances engage more frequently in a wider range of social behaviors provides a new avenue for research on facultative change in competitive strategy based on fluctuating conditions in the social environment. This adaptive link is also the subject of attention in multiple taxa and at multiple levels of analysis (e.g. Wiebe 1995; Mautz and Jennions 2011). Such tactics are of particular interest in phenotypically plastic organisms due to their overt influence on individual morphology, which in turn influences the morphology of other individuals (e.g. Furness et al. 2015). Rapid, reversible changes in
individual morphology, physiology, and behavior affect the hierarchical arrangement of communities (Witham et al. 2003; Smith et al. 2015). *A. burtoni* is useful as a model organism in this burgeoning area of study due to the complex and conspicuous influence of individual male behavior and morphology on other individuals, particularly in regard to reproduction (e.g. Clement et al. 2005; Oliveira et al. 2005; Desjardins et al. 2012).

Although not specifically tested here, it is conceivable that INT males can be identified as those transitioning to or from DOM/territorial/reproductive status. Such individuals have been described previously as expressing physiological changes associated with behavioral changes during social ascent and descent (e.g. Hofmann et al. 1999; Burmeister et al. 2005; Parikh et al. 2006; Maruska and Fernald 2010; Maruska et al. 2012). Bi-directional transitioning between SUB and DOM status depends on environmental and social context (Hofmann et al. 1999; Hofmann et al. 2001; Clement et al. 2005; Fernald 2007; Desjardins and Fernald 2008; Korzan et al. 2008) as well as on growth rate (Hofmann et al. 1999). Moreover, transitional males exhibit increased intrasexual aggression, and body pigment more similar to DOMs within hours of increased intrasexual victory and corresponding increased androgen circulation (Parikh et al. 2006). Thus, the high CI scores of INT males described here may illuminate the behavioral mechanisms and costs during transition from SUB to DOM status.

**Why do INT males ignore threats?**

Our data show that males with DI scores near zero engage more frequently in intrasexual conflict (having the highest CI scores), and engage in a wider variety of conflict behaviors, than either prototypical SUB or DOM males. This trait is consistent with the necessity to adjust most rapidly
to unstable social circumstances. The transition from SUB to DOM status requires vigilant testing and/or observation of DOM males (Desjardins et al. 2012). Therefore, these males must have a mechanism for defraying costs of aggression from DOMs.

These unique challenges may explain the higher frequency of the ignore threat behavior in INT males relative to prototypical SUB and DOM males. Ignoring threats may be a strategy for avoiding risk, testing competitors or competitive events without risk to status (e.g. Judge and De Waal 1993; Grosenick et al. 2007). A male ignoring threat avoids both escalating a contest and the conspicuous social defeat of fleeing behavior. This interpretation is supported in Fig. 4c, where we demonstrate that INT males ignoring threats most frequently do not deliver threats most frequently. As such, these males are likely better equipped to handle confrontation than prototypical SUBs and may ignore threats to better assess relative threat level of an opponent.

Partly due to bright coloration and larger size, males transitioning to or from DOM status are not likely to avoid attention from threatening individuals as effectively as prototypical SUBs (Greenwood and Fernald 2004). Males transitioning between social states (near zero DI) may benefit from more frequent tests of rivals and therefore engage in more confrontations than either prototypical, more submissive SUBs or prototypical, more established DOMs. Threats by rivals may not be successful, in which case energy, social spacing, and status (along with the corresponding hormonal suite) may be conserved by not engaging in stress-based escape or escalated aggression. Interestingly, Fernald and Hirata (1977) describe a behavior comparable to (or the same as) ‘ignore threat’, where males in the process of establishing a territory may fail to flee or fight when attacked.

By definition SUB males have the lowest ratio of wins to losses in intrasexual conflict. A prototypical SUB remaining in place (or ignoring threat) during a confrontation may be at greater
risk of attack and defeat than any other male doing the same. Additionally, DOM males risk acquired territory/status in a given confrontation (e.g., their reproductive status), and a passive response may be much costlier to this group than to any other. In contrast, INT males have higher win/loss ratios, but no territories to defend. In these ways they are uniquely situated as being more capable of winning confrontations than prototypical SUBs, with less to lose in defeat than prototypical DOMs.

Facultative behavioral response to competitor rank has already been demonstrated in *A. burtoni* males, consistent with our hypothesis regarding the ignore threat behavior. An attention hierarchy has been demonstrated in this species, where individuals observe competitive third party interactions and modify their behavior accordingly (Grosenick et al. 2007). Individuals may hasten social ascent and maximize the window of reproductive competence by picking and choosing their fights based on these observations of other males (Desjardins et al. 2012). The range of behaviors involved in this picking and choosing may be expanded by our findings and their expansion on the behavior observed in Fernald and Hirata (1977). Males approaching DOM status have different opportunities/capacities for reproduction (Fernald 2007; Renn et al. 2009; Kustan et al. 2011). It is likely that the threat presented by competitors will vary correspondingly (Hofmann et al. 1999; Maher and Lott 2000; Greenwood and Fernald 2004), and so a behavioral mechanism for varied response should exist.

**How do INT males use pigment displays?**

**Lachrymal stripe display**
The lachrymal stripe is associated with territorial acquisition and agonistic behavior (Heiligenberg et al. 1972; Desjardins and Fernald 2008; Desjardins et al. 2012), suggesting that a dark lachrymal stripe may be an honest signal (Zahavi 1993) of conflict ability. Our data support that association in showing that the display is most frequent in prototypical DOMs. These males would be most likely to consistently win confrontations (e.g. Hofmann 1999; Dugatkin and Druen 2004; Dugatkin and Earley 2004; Oliveira et al. 2002; 2005) thereby increasing tenure as DOMs. However, INT males may also display lachrymal stripes clearly distinguishing them from the prototypical SUBs.

INT males engage in more confrontations, with less certain outcomes, than other males, and so may benefit from activating or deactivating the signal based on a rival’s relative competitive status. Intrasexual confrontations which are evenly matched or in which a male is victorious increase androgen expression, and logically will increase expression of the androgen-correlated lachrymal stripe (Muske and Fernald 1987). Oreochromis mossambicus, another cichlid species, has been shown to increase androgen expression during display against a mirror reflection (an evenly matched fight) and to experience a “winner effect” similar to that of fish victorious in intraspecific combat (Oliveira et al. 2005; Dijkstra et al. 2012).

**Vertical stripe display**

The vertical stripe is a conspicuous visual signal, which can be darkened and lightened moment-to-moment (Fernald and Hirata 1977; Fernald and Hirata 1979). Vertical stripes cover a large area on the lateral body (Fernald and Hirata 1979) and may be displayed as a signal of social defeat, conspicuous to an attacking male. *A. burtoni* males are believed to visually assess the
relative strength of competitors (Desjardins et al. 2012). By exhibiting the vertical stripes as a submissive signal, defeated males might curtail further agonism (Desjardins and Fernald 2008). Thus the fact that INT males show the highest number of agonistic interactions (i.e. high CI), but also exhibit vertical stripes more frequently than other males might suggest that this display provides a tactic for avoiding costly attacks by submitting (Fig. 6a, b).

Variations between SUB and DOM phenotypes on dimensions of reproduction, stress response and social ecology have been described (Ferno 1987; Fox et al. 1997; White et al. 2002; Clement et al. 2005; Parikh et al. 2006; Korzan et al. 2008). It is also important to consider nonlinear variation in these traits during transition, as suggested by the findings of Fernald and Hirata (1977) where wild *A. burtoni* males exhibited unique responses to aggression while establishing territory.

As such, INTs may represent males transitioning in territorial status (Hofmann et al. 1999). These males do not only occupy a central place on the spectrum of some traits expressed in nonterritorial and territorial males, but also exhibit some traits with greater frequency than both prototypical SUB and DOM males. Indeed, tactics used by these transitioning or uncertain individuals may not match with the needs and traits of more subordinate or more dominant individuals, as manifest in traditional hierarchical classifications (e.g. Drews 1993), particularly as pertains to behavioral and social plasticity. The heightened behavioral plasticity in a competitive context of individuals experiencing greater fluctuation in social circumstance may demonstrate the adaptive value of facultative strategies under such conditions; (e.g. Wiebe 1995; Mautz and Jennions 2011) particularly as pertains to the energy expended on territorial maintenance behaviors (e.g. Lederer 1981). Phenotypically reversible organisms exhibit direct and cyclical links between and among behavioral variation, morphology, and the composition of
social groups. These uniquely conspicuous connections provide a valuable avenue for analysis the way in which short term intraindividual and intrapopulation changes in social behavior influence long term behavioral, ecological, physiological, and epigenetic traits (e.g. Oliveira 2012).

In conclusion, we show that modified ethograms for male A. burtoni allow for classification of additional behavioral phenotypes beyond a strict SUB-DOM dichotomy, more fully capturing the complex social dynamic of this model organism. More broadly, using cluster analysis based on intrasexual conflict behaviors and facultative competitor testing or risk avoiding strategies might allow for a more nuanced understanding of social hierarchies in many species.

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Conflict of interest:
The authors declare that they have no conflict of interest. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. The regulations of the Hunter College, CUNY IACUC were followed at all stages of this study.

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Varied effort in rescue by colony mates of experimentally trapped naked mole-rats

Corresponding Author: Andrew Fulmer.
Postal Address: 220 West 148th St., apt. PHA, New York, NY, 10039.
E-mail: Afulmer@gradcenter.cuny.edu
Telephone Number: 1 (917) 734-5353

Running Heading: Rescue behavior in naked mole-rats

Andrew Goldklank Fulmer*, Tatsiana Dzedzits¹, Dan P McCloskey PhD¹,²,³

¹The Graduate Center of the City University of New York, Animal Behavior and Comparative Psychology, Doctoral Program in Psychology, The City University of New York, 365 Fifth Avenue, New York, NY 10016-4309, USA. (A.G.F., T.D.)

²Center for Developmental Neuroscience, The College of Staten Island, 2800 Victory Blvd. Staten Island, New York, 10314, USA (D.P.M.)

³The Department of Psychology and Program in Developmental Neuroscience, The College of Staten Island, 2800 Victory Blvd. Staten Island, New York, 10314, USA (D.P.M.)
We find evidence that Naked Mole-Rats (*Heterocephalus glaber*) accelerate excavation behavior to “rescue” trapped group members. Effort expended (defined by time spent in rescue and initiation of rescue events) varies both by caste and individual. Two colonies equipped with subcutaneous RFID tags were exposed to a trapped-group-member scenario in two permutations. In the first permutation one artificial “cave-in” was created in a single tube attached to the housing enclosure of each colony, with trapped individuals or empty space at the distal end of the tunnel. In the second permutation a bifurcated tube was attached to present trapped individuals or empty space simultaneously. RIFD tagging permitted the time of excavation and identity of excavating rescuers to be recorded with good temporal resolution. Speed of excavation for live animals was faster than speed of excavation for empty space. Queens expended less effort than workers in rescuing colony members. Individuals initiating rescue events were also the most frequent actors during those events.

Key words: Caste, Eusociality, Naked Mole-Rat, Rescue Behavior

*Correspondent: afulmer@gradcenter.cuny.edu*
Introduction: The active decision to “rescue” an experimentally trapped conspecific has been demonstrated in rats, and considered evidence for a homologue to empathy (Ben-Ami Bartal et al. 2011). Active, directed rescue behavior has also been recorded naturally and experimentally in a eusocial insect; the ant *Cataglyphis cursor* (Nowbahari et al. 2009), and under natural conditions in two non-human primates; the capuchin monkey *Cebus capucinus* (Vogel and Fuentes-Jiménez 2006) and the gray mouse lemur *Microcebus murinus* (Eberle and Kappeler 2008). A similar cognitive system could be expected in the naked mole-rat (*Heterocephalus glaber*), a species evolved for life in complex subterranean colonies. In such colonies the ability to overcome physical barriers between individual members would have particular adaptive salience.

It has been suggested that the expandible, intergenerational nest is a pre-requisite for the evolution of eusociality (Andersson 1984; Alexander et al. 1991). Eusocial systems occur in at least four separate insect lineages, one crustacean, and one mammalian (Duffy 1996) Several of these forms, including the naked mole-rat, have solved the “expansible nest” question with a fossorial lifestyle. This lifestyle is often reliant on tunnels to expand the nest, and so the danger of tunnel collapse is inherent to the system. Tunnel collapse may be a factor in dispersal of the reversibly sterile naked mole-rat (Alexander et al. 1999), suggesting that worker retention may be dependent on removing substrate during a tunnel collapse event, which has isolated one or more workers from the colony. We investigate the relationship between rescue behavior (Ben Ami-Bartal et al. 2011) and differential efforts from colony members in the retention of colony mates in the naked mole-rat.

*H. glaber* provides an opportunity to investigate rescue behavior in a social context. Colony members are capable of recognizing a large number of individuals using scent and possibly vocal
cues (Clarke and Faulkes 1999; Cooney and Bennett 2000; Mateo 2003; Holmes and Mateo 2007). Colonies are maintained by prosocial contributions from weaned members, with effort expended on cooperative tasks divided among individuals and varying by caste (Lacey and Sherman 1991). Prosocial contributions include behaviors such as food-source recruitment, territorial defense, co-resting or huddling, substrate movement and tunnel excavation (Yahav and Buffenstein 1991; Judd and Sherman 1995; O’Riain and Jarvis 1998). By definition, the most unique contributions to the colony are made by the queen, by which the colony is defined and created (e.g. Alexander et al. 1991; Lacey and Sherman 1991). The polyethic, caste-like social system of *H. glaber* (e.g. Ziporyn and McClintock 1991) suggests that individuals will also vary in the cooperative behavior of trapped colony mate retention.

Theories of apparently cooperative behavior predict several lines along which this variation may occur. Among naked mole-rats, “lazy” or reluctant helpers have been shown to receive higher rates of aggression than industrious workers, and aggression reinforces cooperative behavior (Reeve 1992; Jacobs and Jarvis 1996). This structure is similar to a “pay-to-stay” model of social contribution (e.g. Kokko et al. 2002; Bergmüller and Taborsky 2005). Similarly, the premise of social prestige (e.g. Zahavi 2000) suggests that animals will increase energetically costly contributions to the group to improve or maintain social status. In this second model, individuals will compete to provide assistance to other group members. It is also plausible that certain individuals are behaviorally predisposed to high excavation behavior as a component of a polyethic system, as seen with other cooperative behaviors in eusocial species (Beshers and Fewell 2001).

The cave-in scenario, whereby members of a colony become isolated by a physical barrier from the colony proper, presents an excellent opportunity to examine the variation in effort expended
to retain individuals. This research presents the results of an experiment to test individual variation in time spent rescuing colony mates and time spent trapped, before being rescued by colony mates.

**Materials and Methods**
Mole-rats were maintained in the facilities and captive colonies at the College of Staten Island, CUNY, in accordance with ASM (Sikes et al. 2011), IACUC and USDA regulations. All of the work reported in this paper was conducted in accordance with relevant laws and animal care regulations. Two captive colonies of naked mole-rat were used in the study, containing four and five individuals, respectively. The small size of these colonies, accounted for by the early and unexpected deaths of the breeding males, allowed for repeated analysis of the role of each colony member as both trapped and rescuing member. Each colony contained one adult female in physiological readiness for reproduction (pronounced genitalia, elongated spine): defined here as the colony queens. Animals were housed in a low-light environment maintained between 76 and 89 degrees Fahrenheit. Enclosures were a series of cages connected into a simulated burrow structure by polycarbonate tubing, and having nearly-air tight connections, increasing the similarity to the mole-rat’s xeric naturalistic environment. Animals were fed *ad libitum* on a mixed diet of tubers, fruits and Teklad Global 2019 lab chow (Harlan). RFID tags (Trovan Unique©) were implanted subcutaneously in all animals. RFID tagging permits measurement of social spacing and association patterns in animals, as well as general movement and locational data.

The statistical analysis was performed using SPSS v.22.0 (SPSS Inc, Chicago, IL, USA). Normality of data distribution was assessed by Kolmogorov-Smirnov test. Nonparametric
alternatives for parametric statistics were used when appropriate. Pearson correlation coefficient was calculated to evaluate association between two interval variables. Phi coefficient was calculated to measure a degree of association between two binary variables. Chi-Square test was used to investigate relationship between to nominal variables. Jonckheere’s test was applied to assess trend in data. Mann-Whitney U (for two independent groups) and Kruskal-Wallis tests (for three independent groups) were used for between-group analysis. The significance level was $\alpha=0.05$. When multiple Mann-Whitney U tests had to be performed to follow up Kruskal-Wallis test, a Bonferroni correction was applied and all effects were reported at $\alpha=0.0167$.

Choice “Rescue” Task

Figure 1 provides a schematic of the testing environment. In this case, a "T" shaped tube was attached to the central colony, with barriers of plastic (removable by experimenters, but not by mole-rats) and cork (removable by mole-rats) between the trapped individual and the colony proper. The plastic barrier was inserted between the trapped individual and the cork, preventing the trapped animal from freeing itself or participating in the rescue effort by any means other than signaling. Barriers were permeable to scent, sound and vibration (assumed to be the three primary modalities of mole-rat social signaling). The plastic barrier was removed by the experimenters as soon as it was reached by “rescuer” mole-rats, to prevent learned helplessness (sensu Ben-Ami Bartal et al. 2011). Animals were trapped in a sequence produced by a random number generator, to mitigate effects of order. A control condition in which experiments proceeded normally but no animal was removed from the colony or trapped in the cave-in tube was used in each set of trials. Six sessions were conducted on two colonies, with each session consisting of one trial with each member of the colony in the trapped condition, along with an
empty control. The “T” shape offered “rescuer” individuals two options: to excavate cork blocking an empty tube, or to excavate cork blocking a tube with an experimentally trapped colony member. The position of the “live animal” tube was randomized for each trial to avoid practice effects. One RFID reader (hereafter reader 1) was placed at the end of the cave-in tube proximal to the main colony, before the cork barrier. A second RFID reader (hereafter reader 2) was placed at the distal end of the colony, on the opposing side of both cork and plastic barriers. The trapped mole-rat was inserted into the tube at the reader 2 end, and the record of the trapped individual’s introduction, taken by reader 2, was considered the beginning of the experiment’s duration. The first encounter of a colony animal with the cork barrier, as recorded by reader 1, marked the beginning of that individual’s “rescue” activity. Only once the trapped animal had passed through reader 1 was the rescue considered complete. The time each animal spent trapped and the time each animal spent engaged in rescue behavior was recorded for all sessions.
Simple “Rescue” Task

The methods used in the Choice “Rescue” Task were also used in the Simple “Rescue” Task, using the same individuals. For simple “rescue” manipulations, each animal in turn was experimentally trapped in the distal end of a single, straight tube adjoining the central colony. Figure 2 provides a schematic of the testing environment, which was a temporary extension of the regular housing environment. Excavation behavior in each tube was measured using the same RFID reader array as in the Simple “Rescue” Task, and the same data collected.
Results

Choice “Rescue” Task

The “branch” of the T shaped tube containing a live animal was excavated first in a significant number of cases (Fig. 3). Pearson Chi-Square test revealed a significant association between the side of the tube and the excavation order ($X^2 = 21.333, p \ (1\text{-tailed}) < 0.001, d.f. = 1$). The odds of being excavated first were 6.76 times higher for the side of tube with a trapped animal than for the empty side.

The results also demonstrated a maintained involvement of excavating by the individuals who discovered the "cave-in". Animals initiating the rescue event (the first to enter the tube) were
significantly more likely to spend the most time engaged in rescue for that event ($\phi = 0.303, p = 0.001$).

**Fig. 3.** Number of trials in which the side of the tube (containing a live animal or an empty side) was excavated first. *** represents a significant difference.

*Simple “Rescue” Task*

The presence of a live animal behind cork barrier significantly increased excavation speed by colony members from the empty control condition (Fig. 4). Mann-Whitney U test showed that it took significantly more time to complete rescue in control condition compared to condition when a live animal was trapped in the tunnel ($U = 194.5, z = -2.089, p (1-tailed) = 0.018, r = -0.259$).
Fig. 4. Mean time (+/- SE) to complete tunnel excavation in control condition and when a live animal was experimentally trapped behind cork barrier. *represents a significant difference ($p < 0.05$).

The caste or reproductive dominance status of an animal was also associated with a significant shift in time needed to complete rescue. Jonckheere’s test revealed a significant trend in the data: time to complete rescue increased from test condition with trapped queen to trapped worker, to being the highest in control condition (Fig. 5) ($J = 765$, $z = 2.66$, $p$ (1-tailed) = 0.004).
Fig. 5. Mean time (+/- SE) to complete tunnel excavation in three experimental conditions: control, trapped queen, and trapped worker. ** represents a significant difference between two conditions ($p = 0.01$).

A Kruskal-Wallis test showed that time to complete rescue was significantly affected by test conditions ($H (2) = 6.752, p = 0.031$). Mann–Whitney U tests with a Bonferroni correction (0.0167 cutoff) were used to follow up this finding. Time to complete rescue did not differ between conditions when workers or queens were trapped ($U = 168.5, z = -1.647, p (1-tailed) = 0.051, r = -0.226$) or between trapped worker and control conditions ($U = 162, z = -1.786, p (1-tailed) = 0.037, r = -0.245$). However, trapped queens were excavated significantly faster than empty tunnels (control condition) (Fig. 5) ($U = 32.5, z = -2.285, p (1-tailed) = 0.01, r = -0.466$).
Additionally, the amount of time an individual spent engaged in rescue varied significantly between the castes, with queens providing some, but much less, rescue attention than workers (Fig. 6) \((U = 179, z = -1.771, p \ (1-tailed) = 0.039, r = -0.241)\).

There was a trend approaching significance for individuals initiating rescue events to be the most frequent rescuer for those same events in the simple rescue task \((\phi = 0.169, p = 0.079)\).

**Fig. 6.** Mean time (in % of total duration of tunnel excavations per trial) (+/- SE) each caste spent engaged in rescue behavior. * represents a significant difference \((p < 0.05)\).

**Discussion**

Our results represent the first evidence of modified excavation behavior by naked mole-rats to “rescue” trapped colony mates. Specifically, we show that in an experimentally contrived “cave-in” scenario, where a novel tunnel is blocked by a removable barrier, the presence of a trapped animal increases excavation speed relative to excavation speed of an empty tunnel with the same
removable barrier. We further show evidence of individual variation in rescue behavior: queens engage in less rescue effort than other members of the colony. Among workers, there is significant variation in rescue effort, with initiators of rescue events also spending the most time in that excavation event.

Nowbahari et al. 2010 put forward four defining characteristics of “rescue” behavior: first, that the animal in need of rescue will remain in a state of distress unless the rescue behavior is performed; second, that the rescuer will be at risk in rescuing the victim; third, that the rescuer enacts a behavior which is relevant to relieving the victim of distress, and fourth, that there is no immediate reward to the rescuer. In this study, trapped animals remained in a state of distress unless rescued (anecdotally assessed based on frequent digging motions and physical inability to return to the main colony area), rescuers expend time and energy, entering a novel area, and behave in a manner consistent with relieving the victim’s distress, with an enhanced rescue speed for queens, suggesting that energy spent is tailored to the individual as well. There is no apparent immediate benefit to the rescuer, apart from any potential social benefit that may be accrued through social prestige (Zahavi 2000). The apparent motivation to rescue by colony members was supported by the differences in excavation effort dependent upon the contents of the trapped chamber (empty or containing a colony mate) in the first study, and the significant preference for the chamber containing the live animal in the second study. Animals varied individually and by caste in effort expended.

Our results may represent an instance of the pay-to-stay hypothesis (e.g. Kokko et al. 2002; Bergmüller and Taborsky 2005) or the prestige principle (e.g. Zahavi 2000) at work. In a pay-to-stay model, lazy workers may be “punished” through imposed costs or evicted from the group entirely, while helping behaviors may be reinforced with prosocial behavior from other
colony members (e.g. Bergmuller et al. 2007). The behavioral repertoire of naked mole-rat workers prominently includes tunnel excavation (Yahav and Buffenstein 1991; Judd and Sherman 1995; O’Riain and Jarvis 1998 and as shown in our results). If such a system is at work in this case, our results suggest that “eviction” may be the negative extreme of a spectrum of priority placed by the group on the retention of the individual; retaining a central individual such as a queen will be of greater priority to the colony than the retention of a worker.

Another explanation, not mutually exclusive, is offered by the prestige hypothesis, where high frequency helpers provide an honest signal of quality (e.g. Zahavi 2000). In social system with extreme reproductive skew and the opportunity for succession, increased social centrality and continuous signaling of high quality may provide long-term benefits by increasing the chances of successful competition for the role of a reproductive. Among mole-rats, female succession to reproductive status is infrequent (Jarvis 1991; Lacey and Sherman 1991; Clarke and Faulkes 1997) while males may have more frequent opportunities (Jarvis 1981; Clark and Faulkes 1999).

In this case social prestige, a long-term mechanism for increasing reproductive opportunities (Bergmuller et al. 2007) may be valuable. If this theoretical framework is applied, our results might suggest active feedback of benefits from social prestige, beyond reproductive activity; animals with more regularly signaled fitness may be adaptively retained with greater priority by other colony members. Our finding that queens do not expend as much energy on rescue as workers is inconsistent with a social prestige paradigm.

Both these theoretical models may additionally be supported by our finding that the initiators of rescue events spent the greatest amount of time excavating in those rescue events. In the pay-to-stay model, these individuals may be hard workers, facultatively avoiding punishment or social isolation by increasing work effort and maintaining greater vigilance. If these same energy
expensive behaviors; maintaining vigilance and investigating disruptions (manifested as initiating the rescue event) and acting most frequently among colony members to complete the excavation associated with the rescue, positively correlate with the social status of individual mole rats among the worker caste, we might find evidence for a prestige model. Additionally, we would find support for this model if individuals appeared to compete for these roles. Taken into account with our data that queens expend the lowest effort, however, we suggest that initiators/highest excavators are demonstrating usefulness to the colony in a pay-to-stay paradigm. Without more precise data on the variation in age or relative strength/body fitness of individuals, we cannot speculate on the presence of either temporal (age-based) or morphological (body structure based) polyethism (Beshers and Fewell 2001).

Our data demonstrate the social variation of contributions to rescue behavior. All colony members, once trapped, elicited heightened excavation behavior relative to an empty tunnel, supporting the concept of directed rescue efforts. Queens engaged in less rescue behavior than workers, and workers initiating rescue events consistently engaged in more rescue behavior for those events than did others. Whether this finding fully fits the description of social prestige or pay-to-stay paradigms requires further research, but we provide evidence that differential effort is spent on the retention of group members in a rodent system; what we hope will be a valuable expansion on the ecology of rescue behavior.

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Literature Cited


Prospectus

The central theme of this work is the adaptive relationship between fluctuating environmental circumstance and facultative variation in behavioral tactics. Environmental and ecological variation between breeding events is linked not only to imbalance in laying capacity and optimal clutch size, but to the availability of suitable hosts (both conspecific and heterospecific) for brood parasitic birds (e.g. Krüger and Davies 2002). The suitability of a host and need for brood reduction and/or evolution of an alternative strategy, rely on the fitness costs incurred by, or benefits to, individual potentially parasitic parents, as described in chapter 1. (Fulmer and Hauber 2016). The simultaneous presence of relatively neophilic and relatively neophobic individuals in a given population has adaptive value under uncertain circumstances, particularly in areas where reproductive territories and/or nutritional resources fluctuate regularly (e.g. Greenberg and Mettke-Hofmann 2001). The ability to adapt to novel circumstances may be linked to social competition under such conditions, as explored in chapter 2, which focuses on Arabian Babblers (*Turdoides squamiceps*); cooperatively breeding birds with high reproductive skew linked to early life social dominance living in arid habitat with annually fluctuating resources (Zahavi 1990; Anava et al. 2000; Kalishov et al. 2005). We find that neophilic behavior towards novel neutral stimuli is positively correlated with early life social dominance. Stimuli in this experiment are considered neutral because they do not mimic a threat or a nourishing stimulus (Fulmer et al. 2016).

At the level of interindividual communication, chapters 3 and 4 focus on the role of behavioral plasticity within individuals as a result of uncertain or fluctuating social, rather than environmental, conditions. Chapter 3 examines autopreening as an example of a displacement behavior (e.g. Tinbergen and Van Iersel 1946) in hierarchically uncertain situations. In this way,
it may represent a third social option under uncertain social conditions: neither avoidance nor approach. The individual engages in the allopreaming event, but delays doing so while also avoiding active resistance. Chapter 4 examines males in a traditionally dichotomous hierarchy which may represent a third, behaviorally distinct, hierarchical cluster. Males of the phenotypically reversible cichlid *Astatotilapia burtoni* alter morphology and reproductive status based on intrasexual conflicts. We show that males likely to be in transition between dominant/territorial and submissive/non-territorial phenotypes exhibit greater social plasticity in these conflicts than do other males, in particular showing a behavior which may also function as a “third” social option in contexts where engaging in conflict is not necessarily beneficial but fleeing from conflicts is not necessary.

The interaction of individuals, competitive and/or cooperative, is at the core of behavioral science. The evolutionary trajectories that have led to the massive diversity of social systems across taxa have been a central topic in zoology, evolutionary biology, and animal behavior throughout the histories of these fields (e.g. Darwin 1859; Hamilton 1964; Zahavi 1995). Many theories have been proposed to explain the adaptive value of apparently cooperative behavior and the principles by which social systems are evolved and maintained (Bergmüller et al. 2007) and while they are often presented in competition (see Zahavi 1995; Clutton-Brock 2002; Bergmüller et al. 2007), these mechanisms may not be mutually exclusive. There is ample evidence that selective pressures differ among and within species (e.g. Stearns 1977) and within individuals (e.g. Yoshimura and Clark 1991). The behaviors of an individual organism that best promote fitness change in environmental context and as a result of varied experience during development (e.g. Buchholz and Clemmons 1997, Sih et al. 2004).

The ontogenetic experience of an individual necessarily influences the structure and
mechanics of the population to which it belongs. To adequately explain this relationship, it is important to allow for a variety of theories, varying in adaptive value by context. Tinbergen’s four questions remain pertinent here. We must consider phylogeny and adaptive value, ontogeny and physiology, to understand the origins of a given behavior (Tinbergen 1963) and the social system to which it contributes. Though all levels are interconnected, the particular emphasis of the work presented in this dissertation is on the relationship between individual behavioral variation and group and/or population composition.

In Chapter 1 I explore a major evolutionary consequence of both individual energetic experience and population dynamics for parental care strategy. Brood parasitism occurs in a variety of taxa and manifests differently among them. In avian brood parasitism, obligate brood parasitism (OBP) has evolved in approximately 1% of species (Cockburn 2006). Some brood parasites are also nestmate-killers, with young killing their host nestmates either through direct aggression or by outcompeting them for parental resources. Even in nestmate-tolerant brood parasites host young are in competition for resources with parasitic young and often pay a fitness cost as the result of parasitism. This extreme version of nestmate competition has drawn attention to possible links between siblicidal and brood parasitic tactics, with support found in shared phylogenetic, morphological, and behavioral traits between OBP and siblicidal taxa (e.g. Spottiswoode and Koorevaar 2012; Wang and Kimball 2012). In this chapter we present a theoretical evolutionary trajectory from siblicidal behavior to both OBP and conspecific brood parasitism (CBP) as well as between CBP and OBP.

The model (see Fig. 1.1) presents a set of conditions based on the resources available to an individual that make brood reduction adaptive, based particularly on fluctuation of resources between breeding events and seasons. When these fluctuations are predictable, obligate sibicide
may be the most appropriate form of brood reduction, while unpredictable shortages correspondingly lead to facultative siblicide. When the cost to inclusive fitness in parasitizing another individual’s nest is lower than the cost to direct fitness of siblicidal offspring, CBP may evolve directly as the mechanism of brood reduction. Where siblicide has evolved as the mechanism of brood reduction, brood parasitism may eventually evolve to defray the major fitness cost of obligate siblicide.

Our model suggests that the cost of heterospecific parental care (due to differences between species in nutritional/provisioning needs, nest structure, incubation tactics, and more) may determine the form of brood parasitism that evolves from obligate siblicide. If a sympatric heterospecific host is available and parasitizing that host does not cost more in fitness due to these differences than offspring lost to siblicide or the inclusive fitness cost of nestmate competition in CBP, OBP will evolve (Fulmer and Hauber 2015). These fitness inequalities described relate directly to the composition, kinship, and environmental experience of populations. This model therefore ties proximate conditions experienced by individuals to ultimate effects on populations, and highlights the influence fluctuating versus stable and predictable versus unpredictable resources have on the evolution of parental and ontogenetic strategies.

An expansion of this modeling approach to address similar and related process in the phylogeny of parasite hosts would be valuable. Brood parasitism is a co-evolutionary process, and it is necessary to consider the influence of parasite on host strategy as well as the influence of host strategies on parasite opportunity (e.g. Kilner 2005). Specifically, future work on this model should investigate the role of kin recognition in egg rejection by conspecific hosts and the imbalance of host care provisioning and parasite developmental need between newly parasitized
heterospecific hosts and their parasites. It would also be valuable to incorporate the length of the coevolutionary relationship between parasite and host into the model (e.g. Soler 2014), as it may better illuminate the thresholds of fitness costs needed for OBP to be adaptive over siblicidal or CBP brood reduction strategies and for host acceptance of parasitic eggs.

In Chapter 2 I provide an example of the pivotal role social experience during brief early ontogenetic periods may play in longer-term later life individual behavioral variation. The adaptive value of neophilia and/or neophobia, depending on context, is well established (Greenberg and Mettke-Hofmann 2001; Smith and Blumstein 2008). Population survival under fluctuating conditions and the dispersal of individuals (and genes) is likely to be influenced strongly by these traits, regulating use of novel resources such as food, nesting sites, and social networks (Boissy 1995; Greenberg and Mettke-Hofmann 2001). Using the individually banded and observer-habituated population of Arabian Babblers (Turdoides squamiceps) from the Arabian Babbler Research Project, I examined neophilic behavior by young birds in a multimodal context. Arabian Babblers form intrabrood hierarchy during the period closely surrounding fledging. This hierarchy remains relatively stable over time, and broader intragroup hierarchy is age-based and similarly stable (Zahavi 1990). As a result, the establishment of intrabrood rank has substantial later life fitness consequences for this cooperatively breeding species with high rank-based reproductive skew. Stimuli used in this research included stationary and moving objects, as well as sound. Each stimulus type had a familiar and a novel condition (Fulmer et al. 2016).

Arabian Babblers are of particular interest in examining the value of neophilia (and/or neophobia) under fluctuating environmental conditions, as the habitat the species occupies is relatively resource-poor. Highly arid desert with unpredictable rains directly connected with food
availability and breeding events (e.g. Zahavi 1990; Anava et al. 2000; Ridley 2007) may enhance the adaptive value of a tendency to locate novel territory and food sources (e.g. Greenberg and Mettke-Hofmann 2001; Smith and Blumstein 2008). Arabian Babblers also engage in producer-scrounger tactics with regard to novel foraging tactics, further supporting the concept of fitness benefits from neophilic behavior in this environment (Keynan et al. 2014). This set of ecological circumstances and behavioral traits is consistent with our finding that all individuals preferred novel stimuli, with higher ranking (and juvenile) individuals being relatively more neophilic (Fulmer et al. 2016).

The link between social rank and neophilia/neophobia has been explored in other passerines with inconsistent findings (Dingemanse and de Goode 2004; Stöwe et al. 2006; Boogert et al. 2006; David et al. 2011). We examined two alternative predictions: one being a risk-averse hypothesis and the other a risk-seeking hypothesis. Taking approach to stimuli of unknown value or threat (i.e. novel stimuli) as a form of risk (e.g. Boissy 1995), we predicted that if individual Arabian Babblers are inherently risk-averse, they would be neophobic, with lower ranking individuals approaching novel stimuli more quickly and more frequently than higher ranking individuals for lack of better options. If individuals are risk-seeking, we predict that monopolization of novel objects is positively associated with social rank, and that higher ranking individuals will more quickly and frequently approach novel stimuli. The latter hypothesis was supported by our findings, with all individuals preferring novelty and a strong positive correlation between intrabrood rank and novel stimulus approach. We also found evidence that adult presence and age positively predicted neophilic behavior, with juveniles being more likely to approach the stimuli than were fledglings (Fulmer et al. 2016).

Intrabrood rank may affect several factors associated with monopolization of desirable
resources. A winner effect may occur, where higher ranking individuals are more certain of a positive outcome in a variety of contexts, and as a result successfully monopolize potentially valuable resources (e.g. Dugatkin and Druen 2004). Individuals may also or alternatively use risk-taking as a status symbol itself (e.g. Zahavi 1990). In future research it would be useful to include body condition as a variable in this context and determine if higher ranked individuals are in fact more physically secure. Presentation of stimuli to isolated individuals outside of a competitive context and controlling for adult presence would also be additive, as it was not possible with free-living individuals. This aspect would be an addition to the experimental design rather than a substitution, as the current design permitted observation of the influence of social inhibition as it would occur in the natural foraging process of the birds. Longer-term fitness consequences of neophilia in this species are also of interest; in this study one highly novelty-seeking young female dispersed successfully before the expected age of two years; a longitudinal study where individuals were tracked for sufficient years to note successful ascent to reproductive dominance in both sexes would add valuable data.

In Chapter 3 I examine the connection between a self-directed and other-directed forms of what is superficially a physical maintenance behavior: auto- and allopreening. Allopreening (and allogrooming) are conspicuous and frequently analyzed forms of apparently affiliative or cooperative behavior (Dunbar 2010, but see Harrison 1965). Using a portion of a long-term dataset collected by members of the Arabian Babbler project from 2002-2004 I demonstrate that autopreening may function as a displacement behavior. Displacement behaviors represent one of the earliest formalized areas of study in modern ethology (Tinbergen and Van Iersel 1946) and function as an explanation for apparently irrelevant behaviors made by individuals in decision-making contexts. Social interaction does not always have a clear positive or negative outcome.
Even interactions traditionally described as cooperative may carry agonistic or competitive signals and social consequences (Harrison 1965; Zahavi 1990). The central findings of this chapter are that undelayed approach by recipients is age-linked, being more likely when actors are older, and positively linked to solicitous behavior by recipients themselves. When recipients have not invited allopreening, approach without delay is significantly more likely. At the same time, autopreening by recipients before making contact in an allopreening event is significantly less likely to be followed by recipient approach to actor. These predictive effects strongly suggest that autopreening is related to social indecision; i.e. it may function as a displacement behavior. Displacement behaviors have been various described as self-soothing (Kinsbourne 1980), involuntary (Wascher et al. 2010), or social signaling behaviors. These explanations may not be mutually exclusive, as a conspicuous display of stress or attempt to self-soothe may have communicative value (e.g. Maestripieri et al. 2007). Socially ambiguous situations must be considered when mapping interactions and decoding the signaling components of behaviors.

Relations based on relative rank and social costs/benefits are often taken as dichotomously positive or negative, with adaptive outcomes distinguishable by the involved individuals, but many situations may arise where this is not the case (e.g. Tinbergen and Van Iersel 1946; Drews 1993; Bergmüller et al. 2007). In this way, social situations that do not have clear costs or benefits (social uncertainty), may become a driver of increased social plasticity. Individuals experiencing greater fluctuation in social relationships – for example individuals either emigrating to new groups or encountering immigrants to a group, or otherwise engaging in interactive dyads with ambiguous hierarchy are likely to employ a wider range of social tactics than individuals in consistent and/or certain social circumstances.

In Chapter 4 I continue on the theme of social uncertainty in hierarchical interactions and
demonstrate the significance of an under-researched male phenotype of the phenotypically reversible cichlid fish *Astatotilapia burtoni* to future research on *A. burtoni* communities. *A. burtoni* is a model organism for physiological and behavioral studies, focusing on social dynamics associated with hierarchy and territoriality (Hofmann et al. 1999). Males undergo rapid and dramatic morphological changes as a result of wins and losses in intrasexual conflict. Traditionally, they are categorized either as territorial (DOM) or non-territorial (SUB) based on the ‘dominance index’ (DI). The DI for each individual is calculated by subtracting the observed count of intrasexual losses from the combined observed counts of intrasexual wins and reproductive behaviors (Korzan et al. 2008). DI roughly corresponds with observable morphological and behavioral changes. Though males actively ascending to or descending from territorial status have been documented and considered as discrete behavioral and physiological phenotypes (e.g. Fernald and Hirata 1977; Hofmann et al. 1999) *A. burtoni* males are frequently described only as DOM or SUB based on a positive or negative score on the dominance index, respectively.

Using cluster analyses (Ward linkage method) this research shows that male behaviors distribute most parsimoniously into three cluster groups; one being similar to prototypical territorial (DOM) males, as described in the literature, one being similar to prototypical non-territorial males (SUB), as described in the literature, and one which exhibits a unique suite of behaviors, engaging in some behaviors more frequently than do either DOMs or SUBs. We categorize these individuals as transitional, or intermediate, males (INT) based on the frequency of their fluctuation between traditional DOM and SUB DI scores and their subjectively assessed morphological phenotype. Additionally, this INT group exhibits DI scores closer to zero than the DI scores of prototypical DOMs and prototypical SUBs. INT males engage in more
confrontations overall than either DOMs or SUBs, but are more likely to win a confrontation (+ DI score) than are SUBs, and more likely to flee from a confrontation (- DI score) than are DOMs. In this way, individuals traditionally ranked as close to zero in DI may in fact be more socially active than more extremely positive or negative ranked individuals. We connect the heightened interactivity and variety of potential outcomes to conflict with two behaviors which are exhibited more frequently by INT males than by either DOMs or SUBs: the reversible pigment display termed ‘vertical stripe display’ and a behavior we term ‘ignore threat.’

The vertical stripe display can be darkened and lightened within extremely short periods and has been associated with stress and submission in intrasexual confrontations (Fernald and Hirata 1977; Desjardins and Fernald 2008). *A. burtoni* males visually assess the strength of potential competitors (Desjardins et al. 2012). Given the relative frequency of conflict exhibited by INT males, we suggest that this cluster may use the vertical stripe as a visual signal of submission, preventing continued attack by competitors. Alternatively or additionally it may more closely link the vertical stripe display with the experience of stress, as the fluctuating circumstances and frequent conflict experienced by INT males may cause these individuals to be more stressed than prototypical SUBs or DOMs. As a goal of this chapter was to provide a non-invasive metric for categorizing and examining the INT phenotype, hormonal assays were not performed. Further work on day-to-day corticosteroid levels (or other metabolic measures of stress) (e.g. Barton 2002) exhibited by males in each phenotype, including those transitioning between phenotypes, will be necessary to explore the connection between the vertical stripe and stress behavior, and the relative experience of stress among the behavioral clusters of males. Of particular note here is the work of Hofmann et al. (1999), which provides physiological measures of males transitioning from SUB to DOM and from DOM to SUB. As in our research, Hofmann
et al. (1999) finds that the exhibition of traits in such individuals is not always intermediate between SUB and DOM.

A second predecessor to this chapter’s focus on the INT phenotype connects with the ignore threat behavior. We define ignore threat as when a “threatened individual does not respond with freezing, flight, or other displacement, but remains swimming/ floating without response visible to the observer” (Chapter 4, Table 4.1). Fernald and Hirata (1977) briefly describe a behavior exhibited by males establishing a territory. These males “would neither flee nor respond to the attack in kind” (Fernald and Hirata 1977, pg. 969) when confronted between established territorial borders. We propose that this behavior is similar or identical to the ignore threat behavior described in Chapter 4, and that INT males exhibit it more frequently than do either DOMs or SUBs as a risk-avoiding strategy. These males are by definition more capable of winning conflicts than are SUBs and less capable than are DOMs. SUBs may need to flee from conflict to avoid injury, and DOMs are less able to do so without incurring costs to territorial status and expressing lower status traits. INT males may be large enough to avoid physical injury if they avoid a direct threat without fleeing, and at the same time avoid descending in status by not expressing submissive behavior or opening themselves up to a potential defeat. In this way they may be able to avoid radical fluctuation in status and phenotype by responding differently to threats than do either prototypical SUBs or DOMs. These findings further support the important role of nuanced hierarchical categorization in analyzing community structure (e.g. Drews 1993), and open up an opportunity to investigate the costs of switching between territorial and non-territorial status in this model species.

Experimental manipulations would improve the codification of the INT phenotype. *A. burtoni* respond to unimodal visual presentations (i.e. mirrors) of potential rivals as though they
are live competitors (Desjardins and Fernald 2010) and may visually assess competitor strength. It would be useful to present digitally manipulated competitors to *A. burtoni* males of each phenotype in isolation; a mechanism which has been used to study social preference and reaction with some accuracy in other teleost fish (e.g. Baldauf et al. 2008). Manipulation should include relative competitor body size and the display of both overall body coloration and the reversible pigment displays described above. The role of the ignore threat behavior as risk avoidant under uncertain social circumstances would be supported if INT males were more likely to ignore threats when presented with “attacking” competitors of similar body size and pigment. Signaling elements of both reversible pigment displays might also be tested in this manner: for example, the lachrymal stripe display as an honest signal of competitive strength would be supported if males are more likely to flee from “attacking” animated rivals with darkened lachrymal stripes, particularly if this effect were at least partly independent from relative body size. If the vertical stripe display is an indicator of and/or response to stress, it might be expected that males will be less likely to flee from, and more likely to attack, an animated rival with darkened vertical stripes. This methodology would thus illuminate the range of facultative competitive tactics employed by males of all three phenotypes, and the relationship of social and competitive plasticity to certainty and uncertainty in intrasexual conflict.

In Chapter 5 I provide exploratory data on the social mediation of rescue behavior in the eusocial Naked Mole-Rat (*Heterocephalus glaber*). Using two small colonies (N = 4, N = 5) and an experimental cave-in scenario, we show that queens spend less time in excavation of experimentally trapped colony members than do workers, and that the individuals most likely to initiate rescue behavior are also the individuals that spend the greatest amount of time performing rescue behavior. This research also demonstrated preferential excavation of tubes in
which colony members were trapped, as compared with empty tubes featuring the same obstacle. While further study of this topic using larger sample sizes is necessary, it represents not only a continuation of rescue studies in rodents (Ben-Ami Bartal et al. 2011), but also an important step in investigating the role of caste in social contribution by a eusocial mammal.

In many cases contribution to the maintenance of the colony by eusocial animals, and particularly *H. glaber* (among the only eusocial mammals) has centered on routine behaviors such as foraging, alloparental care, and nest/tunnel construction (e.g. Lacey and Sherman 1991; Beshers and Fewell 2001). In this case, we test for a stochastic form of contribution: response to the physical isolation of a colony member. Logistical issues prevented the effective implementation of this test with larger colonies, and further research on the subject should attempt to overcome that issue. Future work should include a scenario in which individuals may choose between excavating a food reward or a trapped colony member, colony members of different castes, and a test of signaling modality where scent, sound, and other signals from an isolated animal are presented individually and in various combinations. If a “line of succession” could be identified among females, it would be of particular interest to examine the relative rescue effort exhibited by individuals with greater likelihood of rapid ascent to queen status towards trapped queens versus trapped workers. It might be expected that these individuals stand to benefit from the loss of the queen, or alternatively pose a greater threat to the current queen’s status and must pay to stay (e.g. Bergmüller and Taborsky 2005).

Taken together, the manuscripts presented in this dissertation represent an exploration of a more nuanced assessment of the role of individual ontogeny in determining not only community structure, but also in suggesting which adaptive mechanisms may be most appropriate in explaining those structures. Specifically, they contribute to our understanding of
the ontogenetic and evolutionary tactics prompted by fluctuating and/or uncertain ecological and social conditions. Employ of varied or evolutionary shift in parental care strategies is adaptive when resources pertinent to reproduction, such as nest site availability and resources relative to clutch size, are unstable (as in chapter 1). Early life social experience may influence individuals to respond differentially to novelty in later life (as in chapter 2). A greater variety of social response occurs when the outcome of interactions is less predictable (as in chapters 3 and 4). Individuals vary based on social group membership status (in this case caste) in response to what may be perceived as emergency conditions which temporarily alter the composition of the group (chapter 5). All these findings address the adaptive responses of animals to potentially stochastic conditions.

One significant avenue for exploration of this topic is the concept of the extended phenotype. The premise that the influences a given gene (in combination with other genes) has on the environment are aspects of an organism’s phenotype can theoretically include social behavior and community structure (Wolf et al. 1999). Interindividual variation is a subject of increased focus from work on behavioral syndromes (e.g. Sih et al. 2004), a mechanism for measuring consistent intrapopulation individual variation and relating these findings to community and population experiences. Considering the extended phenotype of an organism in this context – the influence of the gene on individually varied contributions (competitive and/or cooperative) to the social group, and in turn on the environment and community/population – highlights the importance of ontogenetic experience in ultimate-level drivers of variation. Social network analysis will help to clarify the particular effects of such variation in preserving and/or expanding communities and populations, as well as the cyclical influence of group composition (with regard to individuals with different experiential and behavioral traits) on the phenotype of
each member of the group (e.g. Wey et al. 2008; Sih et al. 2009).

With these tools, we are developing a more nuanced and complete picture of the importance of individual development in population structure. This influence can be expected to form a feedback loop where population structure in turn influences the ontogenetic experience of individuals, and the corresponding behavioral suites and reproductive fitness of those individuals.

Further exploration of this topic will be of great value not only to ethology and sociobiology, the burgeoning field focused on behavioral syndromes, and a more detailed and further extended understanding of the extended phenotype, but to conservation. It is well established that the conservation of any species is contingent upon understanding its social needs (e.g. Allee 1931; Komdeur and Deerenberg 1997). Focus on the ontogeny of intrapopulation variation in social behavior and the direct influences of individual social styles on one another and population structure is and will increasingly be a vital perspective for researchers interested in maintaining global biodiversity.

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Appendix 1: Copyright Information


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Animal Behaviour, Intrabrood rank, age and adult presence predict novelty seeking in individual Arabian babblers, Turdoides squamiceps, 114, 2016, 93-99, Andrew Goldklank Fulmer, Peter Santema, Mark E. Hauber, © 2016 Elsevier B.V. or its licensors or contributors. ScienceDirect ® is a registered trademark of Elsevier B.V. With permission of Elsevier.

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