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Ontogeny and symmetry of social partner choice among free-living yellow-bellied marmots

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Affiliative interactions have important fitness consequences for individuals. Yet, precisely how social roles emerge across ontogeny outside of the context of agonistic interactions is largely unknown, particularly in free-living species of nonprimates. Here we used longitudinal data on yellow-bellied marmots, *Marmota flaviventris*, residing around the Rocky Mountain Biology Laboratory in Colorado, U.S.A., to investigate the development of social partner choice in free-living rodents. We first characterized the symmetry of affiliative interactions between mother–offspring pairs and within cohorts of individuals as they developed across discrete life history stages. Affiliative behaviours generally increased in symmetry such that exchanges became more reciprocal as individuals matured. We then evaluated the extent to which individuals biased their affiliative behaviour towards, and agonistic behaviour away from, genetic relatives. As predicted by kin selection theory, rates of affiliation increased with the degree of relatedness among individuals at all three life history stages. Thus, nepotism emerged within cohorts of newly weaned pups and persisted into adulthood despite prolonged annual separations due to hibernation. Surprisingly, close relatives also exchanged the highest rates of agonistic behaviour. After accounting for the degree of relatedness, rates of affiliative behaviours given and agonistic behaviours received remained positively correlated, suggesting that close affiliates are each other's closest competitors. Thus, although reciprocity of affiliative exchanges within cohorts increased as individuals matured, competition among genetic relatives emerged early in ontogeny and persisted into adulthood. Taken together, these results highlight changes in social roles shown by individuals across ontogeny and shed light on theories of life history and social evolution.

A growing body of empirical work on free-living mammals suggests that affiliative social interactions have important fitness consequences for individuals (Silk et al. 2003, 2010; Weidt et al. 2008; Cameron et al. 2009; Frere et al. 2010; Wey & Blumstein 2012). In particular, we are now starting to understand that the early social environment may have long-lasting effects on behaviours that persist into adulthood (e.g. Maestripieri & Mateo 2009; Champagne 2010). Moreover, balanced relationships characterized by reciprocal exchanges of affiliative behaviours importantly enhance the health and life span of mammals, ranging from humans (House et al. 1998) to rock hyraxes, *Procavia capensis* (Barocas et al. 2011), and laboratory rats, *Rattus norvegicus* (Yee et al. 2008). Nevertheless, precisely how free-living animals make decisions with respect to initiating affiliative behaviours and how symmetric exchanges develop across ontogeny remains elusive. For example, the vast majority of studies focusing on the ontogeny of social roles concentrate on the establishment of dominance relationships based on the outcomes of agonistic interactions (e.g. Walters 1980; Holekamp & Smale 1993; Pereira 1995; Archie et al. 2006; Cafazzo et al. 2010; Huang et al. 2011). Those studies that do focus on the ontogeny of nonaggressive behaviours have traditionally focused on domestic (e.g. Ward et al. 2008; Val-Laillet et al. 2009; Pal 2010) or captive animals (e.g. Ralls et al. 1987; Maestripieri 1994; Terranova et al. 1998; Weidt et al. 2008; Toth et al. 2009a). As such, we lack an understanding of the fundamental processes involved in establishing patterns of affiliation among group-mates, especially among free-living species of nonprimates.

Here we investigated the development of affiliative behaviour in the free-living yellow-bellied marmot, *Marmota flaviventris*, a facultatively social rodent for which a complete pedigree and long-term data on behavioural interactions across three discrete life history stages (pups, yearlings and adults) are available. We first describe the development of social roles between mothers and their offspring and then ask whether genetic relationships predict

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the degree to which affiliative and agonistic behaviours are exchanged within groups of individuals occupying the same life history stage. Recent studies on this species revealed that 1-year-olds (yearlings) are generally involved in more affiliative interactions than are adults (Wey & Blumstein 2010). None the less, how these patterns emerge at early stages of development (at the pup stage), the extent to which mothers and other genetic relatives shape these patterns and the relationships between affiliative and agonistic interactions across a lifetime remain unclear.

Hypotheses Predicting Asymmetry of Social Roles across Ontogeny

Mother–offspring interactions

We tested predictions derived from parental investment theory to understand the degree to which parent–offspring conflict arises between mothers and their developing offspring (Trivers 1974; Mock & Forbes 1992). Because mothers trade off between current and future reproduction, we expected mothers to 'disagree' with offspring about the duration of the period of maternal investment. In mammals, such conflict is expected to emerge around the time of weaning, such that pups are expected to seek nourishment or protection from mothers, and hence initiate a greater proportion of affiliative interactions with mothers than vice versa. As offspring forage independently and approach the start of their own reproductive 'careers', theory predicts that they should play a less active role in maintaining affiliative relationships with their mothers than do immature pups. We therefore expected affiliative behaviours between mothers and offspring to become more balanced (increase in symmetry) as developing offspring matured. Because virtually all males but only about half of females disperse as yearlings in yellow-bellied marmots (Blumstein et al. 2009; Armitage et al. 2011), we also predicted mothers to play a more active role in maintaining affiliative interactions with female yearlings than with male yearlings.

Interactions within cohorts

Because sociality enhances fitness in yellow-bellied marmots (Armitage & Schwartz 2000), we next investigated the development of social relationships within cohorts (age-mates) of marmots across each successive life history stage. We focused on the ontogeny of affiliative interactions because age-structured dominance has already been demonstrated for this species; older individuals are socially dominant to younger ones (Huang et al. 2011). If selective partner choice is adaptive (Noë & Hammerstein 1994; Dugatkin & Sih 1995), then we expected newly emerged pups to become more selective in their social choices as they matured. Specifically, we expected the symmetry of affiliative interactions to decline across successive stages as individuals come to understand the relative value of each potential social partner in their group. The overall symmetry of affiliative behaviours might decline if individuals compete for access to the most valuable social partners. Alternatively, if social interactions by immature animals are primarily limited by spatial constraints facing pups that are primarily found at burrows (Armitage 1991), then affiliative exchanges should become more balanced within cohorts after newly recruited animals have 'introduced' themselves to their group-mates and become integrated within their group's social network.

Hypotheses Predicting Relationships between Affiliative and Agonistic Interactions

Kin selection theory predicts that individuals should generally gain inclusive fitness benefits from biasing affiliative behaviours towards and harmful behaviours away from close genetic relatives (Hamilton 1964). This theory should explain maternal behaviour directed towards offspring as well as behaviour directed by individuals of both sexes towards their maternal and paternal relatives. However, the protective value of kinship with respect to curtailing aggression in mammals has recently been called into question (reviewed by Widdig 2007). Alternatively, natural selection might favour selfish behaviours in circumstances during which individuals compete with close relatives through forces such as sibling rivalry (Mock & Parker 1997) or reproductive suppression/competition (Wasser & Barash 1983; Stockley & Bro-Jorgensen 2011). Such competition may give rise to reproductive skew, defined here as the extent to which breeding is monopolized by dominant individuals (Johnstone 2000; Cant 2006). Because there is some evidence of reproductive skew in yellow-bellied marmots (Allainé 2000), individuals might direct aggression towards their close associates, many of whom are also their close genetic relatives, if doing so enhances their own survival and/or reproduction.

Although these hypotheses have been tested extensively in nonhuman primates and social insects, and to a lesser extent in social carnivores (reviewed by Widdig 2007; Hager & Jones 2009; Smith et al. 2010), explicit tests of how affiliative behaviours emerge across discrete life history stages in free-living rodents are generally lacking, with data on eusocial naked mole-rats, *Heterocephalus glaber*, being a notable exception (Jarvis 1981). Moreover, previous rodent studies focused on the frequency of agonistic acts without considering variation in the number of opportunities to attack individuals of various degrees of relatedness (e.g. Kareem & Barnard 1982; Wey & Blumstein 2010, 2012). Previous approaches could potentially yield biased conclusions because close kin (e.g. mother–offspring pairs, siblings) typically spend the most time in close proximity to each other. Additional study is therefore warranted.

METHODS

Study Subjects and Field Site

Yellow-bellied marmots are ground squirrels that occupy geographically distinct areas, called colony sites (Armitage 1991). Colonies of marmots vary in size and may include one or more adult males as well as one to several matrilines of adult females and their immature offspring. Residents therefore vary in their degree of genetic relatedness to each other (Olson et al. 2012). From 2002 to 2011, we monitored individually recognized free-living marmots at colony sites located around the Rocky Mountain Biological Laboratory (RMBL) in Gunnison County, Colorado, U.S.A. The current study was part of a long-term study initiated in 1962 (Armitage 2010). We regularly trapped known individuals in Tomahawk traps set around burrow entrances on a biweekly schedule during the active season. Upon capture, we transferred each marmot into a canvas handling bag to weigh it, sex it and determine its age. We marked individual marmots with eartags and Nyanzol cattle dye and collected a hair sample for DNA analysis at first capture. Marmots were classified into three discrete life history stages, each separated by annual periods of hibernation: pups ($<$1 year old), yearlings (1 year old) and adults (sexually mature animals, $\geq$2 years old). Because pups were first observed above ground after weaning ($\sim$25 days after birth; Armitage 2003a), recording behavioural development prior to the cessation of nursing was beyond the scope of this field study.

Behavioural Data Collection

From April to September, observers monitored each colony site during times of peak activity in the mornings (0700–1000 hours) and afternoons (1600–1900 hours) on most days using spotting scopes from a distance (20–150 m) to avoid influencing the behaviour of the subjects. At each observation session for a given