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Alarm Callers Are Females with Greatest Genetic Representation

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Synonyms

[Cooperation](#); [Dispersal](#); [Nepotism](#); [Partial migration](#); [Philopatry](#); [Primate](#)

Definition

Philopatry is the retention of individuals in the natal group or territory (Ekman et al. 2001). *Kin selection* is a selective interaction between relatives that increases the fitness of the recipient at the expense of the fitness of the actor. Such behavior will be selected if the cost to the actor (c) is less than the benefit to the recipient (b) multiplied by the coefficient of relatedness (r). This can be summarized with Hamilton's law: $br > c$ (reviewed in Silk 2002). *Nepotism* is behavior between relatives through which the actor provides a benefit to the recipient regardless of any increase or decrease in the fitness of the actor (Silk 2002).

Introduction

Philopatry to and dispersal from a natal group is a critical element of any animal's life history and is driven by three primary selection pressures: kin selection, resource competition, and inbreeding avoidance (Moore 1992; Lawson Handley and Perrin 2007). Because these forces are frequently sex specific, philopatry often also follows a sex bias. In female philopatric species, females will be best represented genetically because maternal lineages continue across generations, unaffected by migration patterns.

While a combination of these selection pressures promotes a species-specific dispersal strategy, kin selection is the strongest predictor of dispersal given that relatives can only interact if neither has dispersed from a group (Moore 1992). Nepotistic behavior promotes kin selection and has been observed in a variety of mammal and bird species (reviewed in Lawson Handley and Perrin 2007). For example, in birds, offspring are offered exclusive access to food and defended from competitors by parents (Ekman et al. 2001).

This entry reviews the role of alarm vocalizations as nepotistic behavior in female philopatric species.

Kinship as a Determinant of Alarm Calling

Alarm calling is a prevalent antipredator behavior among many species. Males are typically better suited to defending a group against predators given their larger size and more capable adaptations (e.g., larger canines – Gould et al. 1997). Where the vocal repertoire in a species differs between male and females, males are therefore often assumed to provide the majority of protection from predators; however, the nepotistic nature of any such behavior, including selective alarm calling, has only been tested empirically in a small number of bird and mammal species (Ekman et al. 2001).

In return, immigrant males in female philopatric groups that benefit females with antipredator behavior are expected to be accepted and tolerated within the group. This was found not to be the case in vervet monkeys (*Chlorocebus pygerythrus*), where no sex differences in alarm calling rate were found (Baldellou and Peter Henzi 1992). Similarly, Bolt et al. (2015) found no significant difference in vocalization rates between dominant alpha males and subordinate immigrants in female philopatric ring-tailed lemurs (*Lemur catta*). Instead, male vocalization rates correlated with increased predation risk and temporal vocalization rates of other group members, subsequently interpreted as attempts to confuse predators. This is consistent with Gould's previous study of *L. catta* at the same site in which no difference in vigilance behavior was found between sexes, nor was any relationship found between vigilance behavior and male ranking (reviewed in Gould et al. 1997).

Instead, in other female philopatric primate species, females exhibit higher rates of antipredator behavior than males. For example, Verreaux's sifaka (*Propithecus verreauxi*) females emit alarm vocalizations in response to predators at a higher rate than males (Lewis 2005). In ring-tailed lemurs (*Lemur catta*), alpha females are the most vigilant member of the group, which is consistent with female dominance over typically immigrant males (Gould et al. 1997). Siberian jay (*Perisoreus infaustus* – Griesser and Ekman

2004) alpha females produce alarm calls at a significantly higher rate when in proximity to offspring compared to immigrant males. This behavior not only confers a nepotistic benefit but also suggests that the presence of immigrants is more costly to alpha females than alpha males, possibly because of increased competition.

Intrasexual differences also influence nepotistic alarm calling. In three female philopatric species (vervet monkeys; capuchin monkeys, *Cebus apella nigrinus*; ground squirrels, *Spermophilus* spp.), females with more offspring issue alarm calls in response to predator encounters at greater rates than those with fewer offspring (reviewed in Wheeler 2008). This pattern has been attributed to variation in parental care, as females with more offspring stand to gain greater evolutionary benefit with increased offspring survival.

Conclusion

Where antipredator behavior is nepotistic, it can be considered a behavioral mechanism of kin selection and will select for a sex-biased strategy of dispersal. For example, nepotistic antipredator behavior only benefits the recipient as long as they remain in the natal group or until the actor and the recipient disperse together (parallel dispersal – Lawson Handley and Perrin 2007). Such a benefit would be expected to delay dispersal for recipients of both sexes; however, in species with strong matrilineal hierarchies (e.g., vervet monkeys; baboons, *Papio* spp.; macaques, *Macaca* spp. – reviewed in Silk 2002), this will lead to female philopatry. For example, even where both male and female parents exhibit nepotistic behavior, only female offspring remain in the natal group. Numerous other selection pressures will drive male dispersal in addition to any altruistic trade-offs – for example, low social integration is the primary cause of male dispersal in blue monkeys (*C. mitis*). Similarly, in other taxa, certain costs will apply that lead to sex differences within parental nepotism.

While antipredator behavior is often both observable and empirically testable, nepotistic behavior is not restricted to protection from

predation. Among others, selective infant care by parents (e.g., vervet monkeys) and nepotistic coalition formation to invade mixed-sex groups (e.g., gray langurs, *Presbytis entellus*) have all been identified as altruistic mechanisms of kin selection (Moore 1992). Advances in substantiating primate recognition highlight the role of reciprocal altruism outside of kin. Future behavioral research complemented by work at the genetic level will provide confirmation of the forces driving cooperative behavior and the evolution of female philopatry (Silk 2002).

Cross-References

- ▶ [Alarm Calling Predicted by Inclusive Fitness](#)
- ▶ [Females Remain with Natal Group](#)

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