Animal Behaviour 112 (2016) 83–91

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Kinship modulates the attention of naïve individuals to the mobbing behaviour of role models

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ARTICLE INFO

Article history:
Received 22 July 2015
Initial acceptance 21 August 2015
Final acceptance 22 October 2015
Available online
MS. number: 15-00627R

Keywords:
antipredator behaviour
cooperation
family living
kin group living
nepotism
parental care
predator mobbing
social learning
teaching

The social acquisition of life skills is essential in a wide range of species. Field experiments have demonstrated that naïve young learn particularly from their parents how to deal with predators or how to find suitable food. However, it remains unclear whether the response of young differs in a novel situation when together with related (i.e. parents) or unrelated role models. We addressed this question in a group-living bird species, the Siberian jay, *Perisoreus infaustus*, groups of which can contain both related and unrelated juveniles. Groups are formed around a breeding pair which engages in prolonged parental care, facilitating delayed dispersal of offspring for up to 5 years. About 25% of juveniles are killed by predators during their first year of life, suggesting that predator avoidance is a crucial life skill for juveniles. Exposing groups to perched predator models showed that kinship influenced how juveniles responded to the mobbing behaviour of breeders. Upon exposure to a predator model, related juveniles immediately paid attention to the behaviour of breeders and copied most of their movements. In contrast, unrelated juveniles copied the behaviour of breeders less frequently, but regularly foraged in the presence of a predator model. These results show that juveniles respond differently to parents and unrelated role models, potentially affecting the acquisition of vital life skills. Parental care creates a close social bond, predisposing juveniles to pay attention especially to novel behaviours shown by their caregivers. Furthermore, parents have a fitness benefit from facilitating the skill acquisition of their offspring. Thus, a prolonged parent-offspring association is likely to enhance skill acquisition and influence cognitive evolution across species.

The acquisition of life skills is essential for most animals and much of it involves learning from others (Laland, 2004; van Schaik, 2010). Field studies and experiments have shown that naïve individuals learn from role models how to avoid predators, how to forage or how to choose suitable mates (Danchin, Giraldeau, Valone, & Wagner, 2004; Freeberg, 2000; Galef & Giraldeau, 2001). On a proximate level, social learning ranges from social facilitation where individuals passively benefit from associating with conspecifics to learning that requires active social interactions between individuals (Laland, 2004; van Schaik, 2010). Consequently, social learning is widespread in species with overlapping generations and prolonged associations between parents and offspring (Drobniak, Wagner, Mourocq, & Griesser, 2015). However, the close bond between parents and offspring makes it difficult to examine whether kinship to role models influences the behaviour of naïve individuals in a social learning context.

One of the most important life skills is predator avoidance. It involves the recognition of predators and conspecific warning calls, and the use of appropriate escape strategies (Caro, 2005; Cheney & Seyfarth, 1990; Griesser, 2008; Griffin, 2004). There is a high selective pressure for individuals to respond appropriately during the first predator encounter of their lives. Failing to do so can be lethal and in many species juveniles experience higher predation rates than adults (Caro, 2005; Cheney & Seyfarth, 1990; Griesser, Nystrand, & Ekman, 2006; Newton, 1998). In species with parental care, naïve individuals can acquire or learn to refine these skills from their parents or other role models (Griffin, 2004). For example, infant vervet monkeys, *Chlorocebus aethiops*, give warning calls to both predatory and nonpredatory bird species, but learn to discriminate between these species through observational conditioning from other group members (Cheney & Seyfarth, 1990). Similarly, juvenile Belding's ground squirrels, *Urocitellus beldingi*, develop an appropriate response to warning calls faster when

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http://dx.doi.org/10.1016/j.anbehav.2015.11.020
0003-3472/

reared together with conspecifics. Also, juveniles pay more attention to warning calls from their mother than calls from conspecifics although the reason behind this difference remains unclear (Mateo, 1996; Mateo & Holmes, 1997).

These observations in Belding's ground squirrels raise a crucial but largely overlooked question: does kinship influence how naïve individuals respond to role models in a novel situation? In many species, learning is vertical, meaning naïve individuals can learn from either their parents or other role models (Laland, 2004). Models predict that naïve individuals should learn from any role model, independent of kinship (Rendell et al., 2010). While naïve offspring can interact with other adults in a number of species, such as in many social fish, mammal or bird species, offspring learn mainly from their parents in species with parental care. Cross-fostering experiments have demonstrated that even basic life skills, such as the acquisition of the foraging niche, can be acquired from the social parents (Slagsvold & Wiebe, 2011).

The close social bond between parents and offspring may predispose offspring to learn preferentially from their parents (van Schaik, 2010). Parents should be a reliable source of knowledge since they have a fitness incentive in passing on their knowledge to offspring (van Schaik, Isler, & Burkart, 2012). In contrast, unrelated individuals are usually not as tolerant as parents, preventing juveniles from learning socially, and experienced individuals might use unrelated juveniles as 'cannon fodder' in critical situations (Ekman, 1987). Consequently, juveniles may not pay attention to the behaviour of unrelated role models. Alternatively, if the difference in knowledge between naïve individuals and role models is crucial, naïve individuals should pay attention to the behaviour of role models independent of the social relationship (Laland, 2004; Rendell et al. 2010).

Here, we investigated how naïve individuals respond to related and unrelated role models in a novel situation in a social bird species, the Siberian jay, *Perisoreus infaustus*. Groups are formed through the retention of offspring with their parents beyond independence (henceforth labelled retained offspring) and/or through the immigration of unrelated nonbreeders, mostly juveniles (henceforth labelled immigrants) (Ekman, Eggers, & Griesser, 2002; Griesser, Nystrand, Eggers, & Ekman, 2008). At the time of dispersal, juveniles are nutritionally independent from their parents, but during their first winter they experience a higher mortality than older individuals (assessed by following the survival of 110 radiotagged individuals; Griesser, 2013; Griesser et al. 2006). Predation is the key cause of mortality: accipiter hawks (*Accipiter gentilis, Accipiter nisus*) account for 70% of all deaths and owls account for 25% of all deaths (Griesser et al., 2006). This difference in mortality may reflect that juveniles still lack certain predator avoidance skills.

When they encounter a live perched predator or are exposed to a perched predator model, Siberian jays immediately change their behaviour by moving upwards in trees, approaching the predator by moving from tree to tree and giving a range of different mobbing calls (Griesser & Ekman, 2005). Groups mob the more dangerous sparrowhawk, *A. nisus*, longer than the less dangerous Ural owl, *Strix uralensis*, and breeders in groups with retained offspring give more mobbing calls and mob longer than breeders in groups with immigrant juveniles or no juveniles (Griesser, 2009; Griesser & Ekman, 2005). Most mobbing calls are given by male breeders, and independent of their social rank, males swoop more often over a predator model than females.

While immigrants engage in risky behaviours more often than retained offspring (Griesser, 2003; Griesser & Ekman, 2005), it remains unknown whether kinship influences the response of juveniles to the predator mobbing behaviour of breeders. Earlier studies showed that birds can learn to recognize predators from conspecifics (Curio, Ernst, & Vieth, 1978); thus, we predicted that juveniles would respond to the mobbing behaviour of breeders independently of their kinship. We tested this hypothesis by exposing groups to a Ural owl and a sparrowhawk model, and recording the behaviour of breeders and juvenile group members. Exposing groups to two predator models allowed us to investigate whether the risk posed by a predator and the associated difference in breeder mobbing intensity influence the behaviour of juveniles during mobbing.

METHODS

This study was conducted in a population of Siberian jays that has been studied from 1989 onwards close to Arvidsjaur, Swedish Lapland (Ekman, Eggers, Griesser, & Tegelström, 2001; Griesser, Halvarsson, Sahlman, & Ekman, 2014). Here, we use field data collected between autumn 1999 and autumn 2000. Almost all birds in the study population were individually colour-ringed, aside from three individuals that were never caught. Blood (50 µl) was taken from all caught individuals for molecular sex determination (Griffiths, Double, Orr, & Dawson, 1998). Our experiments adhere to the ASAB/ABS Guidelines for the Use of Animals in Research, the legal requirements of Sweden (where the field work was carried out) and institutional guidelines. The experiments, handling and bleeding of birds was performed under the ethics licence of Umeå djurförsöksetiska nämd (licence number A80-99 and A45-04). Ringing was performed under the licence of the Museum of Natural History, Stockholm. Our experiments involved the exposure of wild birds to models of predator species that occur at the study site. Since we used a natural setting, birds could decide how long to mob the models. We removed the models as soon as the birds stopped mobbing, and groups usually returned to the feeder at the experimental site within 30 min (Griesser & Ekman, 2005).

Predator Experiments

We presented perched predator models to 27 groups that included one to three naïve juveniles about 4 months of age (Table 1). For all experiments, the models were positioned 5 m from a feeder on a 1 m high pole, and concealed with a plastic cover before the jays were attracted to the feeder by whistling (Griesser & Ekman, 2005). Once group members had foraged undisturbed for 15 min, the model was exposed when a randomly selected breeder and nonbreeder were together on the feeder. After the whole group had stopped mobbing and had moved more than 50 m from the experimental location, we covered the model again. For each experiment in the same group, the feeder and the model were placed in a different location near the centre of the territory.

The vocalizations and behaviour of individuals were recorded with a video camera (Griesser & Ekman, 2005), and one of us (M.G.) scored all videos. For 90% of all calls it was possible to assign caller identity unambiguously; unassigned calls were excluded from the analyses (Griesser & Ekman, 2005). The detailed behaviour of all group members was extracted from the videotapes using the categories listed in Table 2. We noted whether or not juveniles moved independently of a breeder (see Table 2 for the specific definitions). Moreover, we recorded all displacements (i.e. an individual is approached and forced away by another individual) among group members during the exposure to the predator models. We recorded all movements of group members from and to the feeder for 5 min before exposure to a predator model to assess whether context influenced whether or not juveniles copied movements of breeders (Table 2).