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Development of a linear dominance hierarchy in nestling birds

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Theoreticians propose that trained winning and losing are important processes in creating linear animal dominance hierarchies, and experiments have shown that both processes can occur in animals, but their actual roles in creating natural hierarchies are unknown. We described agonism in 18 broods of three blue-footed boobies, *Sula nebouxii*, a species for which trained winning and losing have been demonstrated, to infer how these processes generate and maintain a natural hierarchy. Ranks in the linear hierarchy that emerged in every brood were initially assigned by asymmetries in age, size and maturity, which led to differences between broodmates in levels of expressed and received aggression and, consequently, to differences in the training of their aggressiveness and submissiveness. Later, ranks appeared to be maintained by the chicks' acquired aggressive and submissive tendencies combined with ongoing effects of persisting differences in size and maturity. Our results suggest that trained winning and trained losing are important in the construction of booby hierarchies but that these two axes of learning are largely independent. Increase in submissiveness occurs over a period of about 10–20 days, and the level of submissiveness reached varies with the amount of aggression received. After training, submissiveness is apparently maintained by a lower level of aggression and increasing use of threats. Threats become increasingly effective as chicks age, but are never as effective as attacks.

Keywords: agonistic behaviour; blue-footed booby; dominance; hatch asynchrony; hierarchy; *Sula nebouxii*; trained winning

Theoreticians have asked which behavioural mechanisms can in principle efficiently generate the linearity that characterizes many animal hierachies (e.g. Chase 1974; Beaugrand 1997; Broom 2002). Candidate mechanisms include trained winning and losing (Hsu et al. 2006), the learned dyadic behavioural dispositions of true dominance (Bernstein 1981), assessment of fighting ability, and the bystander effect (an individual assesses others by watching them fight each other; Chase 1982a, b; Dugatkin 2001; Chase et al. 2002), and combinations of these mechanisms are expected (e.g. Mesterton-Gibbons & Dugatkin 1995; Beaugrand 1997; Pagel & Dawkins 1997). Mathematical modelling prevails in this field and experimental tests are sometimes made, but testing is done in artificial situations whose relevance to naturally occurring dominance hierarchies in the study species is usually unknown. We lack quantitative descriptions of the emergence of natural animal dominance hierarchies, and further progress in developing and testing ideas about the formation of dominance relationships and the development and maintenance of dominance hierarchies may depend critically on getting to grips with what actually occurs in nature.

Trained winning and trained losing are the two learning mechanisms most widely expected to contribute to hierarchy formation and maintenance (Barnard & Burk 1979; Pagel & Dawkins 1997; Beacham 2003). Although their existence has been demonstrated in experimental tests of diverse species of vertebrates, their actual functioning in the construction of natural dominance relationships and hierarchies is still obscure (Dugatkin 1997). Each individual's history of victories and defeats against its competitors is generally expected to condition it to a particular position on an aggressive–submissive continuum (e.g. Theraulaz et al. 1989), and the relative positions of all group members on the continuum could determine the hierarchy among them. However, assessment is also likely to be important, and, in theory, the nature of a hierarchy can depend on trained winning or trained

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losing, or both, and this is seldom known (Dugatkin 1997). Nor do we have a grasp of the schedules of interactions whereby members of natural groups entrain each other's and their own agonistic responsiveness: in particular, how long training takes and how agonism changes when it has been achieved (Bonabeau et al. 1996).

An amenable subset of animal dominance hierarchies includes those that occur in altricial broods of some avian species (reviews in Mock & Parker 1997; Drummond 2001, 2006), and these can be observed from the start of their agonism. As far as we know, these infant hierarchies do not involve such complications as alliance formation or even individual recognition and they may be among the most simple hierarchies that occur in natural groups of vertebrate conspecifics. Typically, two to four nestlings hatch at intervals of 1–5 days and start attacking each other within several days. The nature of dyadic dominance relationships varies among and within species (Drummond 2006), but nestlings usually sort themselves over a period of several days or weeks into a linear hierarchy that follows the order in which they hatched and confers growth and survival benefits on high-ranking individuals. Our knowledge of the development of these hierarchies is sketchy because broods are rarely observed from the onset of hostilities, the temporal resolution of data is often poor, responses to aggression are seldom quantified and few studies have actually analysed age-related changes in aggression or submission (but see Drummond et al. 1986; Cook et al. 2000; Nathan et al. 2001).

Dominance relationships and hierarchies occur in broods of the blue-footed booby, *Sula nebouxii*, a marine bird that produces broods of one to three altricial chicks that fledge at about 3 months of age (Nelson 1978). Staggered laying and hatching ensures that broodmates differ substantially in age: in three-chick broods, the A-chick is, on average, 4.0 days older than the B-chick, which is 3.6 days older than the C-chick (Castillo Alvarez & Chavez-Peón 1983). Broods of three are largely unstudied, but in broods of two, there is always a dominance relationship, usually with the A-chick assuming a dominant role characterized by daily attacking and threatening, and the B-chick assuming a subordinate role characterized by minimal aggression and submissive responses to aggression (Nelson 1978; Drummond et al. 1986; Anderson & Ricklefs 1995). A-chicks grow faster than B-chicks during the first few weeks of life and are more likely to fledge, but surviving B-chicks catch up on growth and, at fledging, they are just as large as A-chicks.

Experimental pairings of different combinations of unfamiliar dominant chicks, subordinate chicks and singletons (chicks with no broodmate) that were 12–55 days old demonstrated that trained winning, trained losing and assessment are all involved in the agonism of blue-footed boobies. Thus, a chick's aggressiveness or submissiveness to an unfamiliar chick is influenced by prompt assessment of its relative size, but more importantly, by its own agonistic training in its home brood: previously dominant broodmates tend to behave aggressively and nonsubmissively, previously subordinate broodmates tend to behave submissively and nonaggressively (Drummond & Osorno 1992; Drummond & Canales 1998). The effects of trained winning and losing also seem to include modification not only of agonistic tendencies but also of fighting ability: A-chicks dominate unfamiliar B-chicks that are 32% heavier than themselves, even though most B-chicks respond to their newfound size advantage with increased aggressiveness. Hence, the observed stability of dominance relationships over the nestling period (Drummond et al. 1991) could largely be due to trained winning and losing.

We studied the emergence of dominance hierarchies in natural three-chick broods of the blue-footed booby. Broods of three are always a minority and often are reduced by nestling mortality to two chicks, but sometimes all three broodmates survive and cohabit through to fledging. In our study population, 217 three-chick broods fledged 75% of A-chicks, 69% of B-chicks and 31% of C-chicks, and, in 20% of broods, all three broodmates fledged (H. Drummond, unpublished data from 24 seasons). We sought evidence for how the mechanisms of trained winning and trained losing operate in a brood of three to create and maintain a linear hierarchy. We compared the development of behaviour in A-, B- and C-chicks to infer their schedules of training and how they come to occupy their dominance ranks. Examination of their behavioural development also yielded insight into (1) whether aggressiveness and submissiveness are two sides of the same coin or independent axes of behavioural tendency, (2) whether B-chicks acquire intermediate rank by simultaneously learning increased submissiveness to their elder broodmate and increased aggressiveness to their younger broodmate and (3) whether aggressors progressively substitute threats for attacks as victims learn to submit to threats.

METHODS

We located two-chick and three-chick broods on Isla Isabel, Nayarit, Mexico (21°52′N, 105°54′W) in March and April of 2002 and 2004 by monitoring all nests in our study area every 3 days, starting shortly after the start of hatching in the colony. When hatching date was unknown, we estimated chick age using culmen and ulna growth curves of the same population. We banded broodmates according to their age ranks (Drummond et al. 1991). When broods were first found, there was no risk of misidentifying age ranks within a brood, given this booby's large hatching intervals. Blue-footed boobies lay clutches of one to three eggs. Clutches of three eggs are uncommon, but a minority of two-chick broods arise through hatching failure in three-egg clutches.

Sampling of three-chick broods and two-chick broods was constrained by availability and mortality and could not be equitable. Three-chick broods were sampled in 2002 by observing all intact broods of that size more or less daily until the first chick death occurred (all three-chick broods suffered mortality in 2002). We suspended observation and switched to a new three-chick brood whenever switching would assure more even sampling of the first 6 weeks of life. Eighteen three-chick broods were observed for a mean ± SE of 10.2 ± 1.9 days, from A-chick ages of 10–23 days ($\overline{X} = 16.2$ days) to 13–49 days ($\overline{X} = 27.3$ days); in these