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Effect of food deprivation on dominance status in blue-footed booby (*Sula nebouxii*) broods

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A pecking hierarchy is normally established in the usual two-chick brood of the blue-footed booby (*Sula nebouxii*). The senior (first-hatched) chick dominates its smaller sibling and receives a greater share of parentally provided food. Experimental broods were created by putting together two unrelated junior chicks of the same age in a vacated foster nest. The state of the chicks was manipulated by a period of controlled artificial feeding so that each chick underwent a different level of food deprivation. The resulting dominance relationship depended on the relative food deprivation level of the chicks: the hungrier chick normally became dominant. However, the effect of hunger was occasionally overruled by size difference: when the hungrier chick was much smaller than its foster sibling, it was unable to gain dominance over its larger companion. Dominance status is likely to have greater value for the hungrier chick, while the cost of fighting should be lower for the larger chick. These results conform to the evolutionarily stable strategy predicted for games with asymmetric payoff and differences in resource holding power. *Key words:* asymmetric games, boobies, brood dominance, sibling competition, *Sula nebouxii*. *[Behav Ecol 7:82–88 (1996)]*

This experiment investigates the effect of food deprivation on pecking hierarchies between blue-footed booby (*Sula nebouxii*) nestlings. Within-brood hierarchies during the nestling period are established in a number of bird species (Bryant and Tatner, 1990; Edwards and Collopy, 1983; Mock et al., 1990). In two-chick broods of the blue-footed booby (two eggs is the most common clutch size in this species, Drummond et al., 1986), the senior (first-hatched) chick, on average four days older than its junior sib, normally becomes agonistically dominant over this latter one (Drummond et al., 1986; Nelson, 1978). The dominant chick has greater access to parental feedings and grows faster than the subordinate chick, especially during the first few weeks of the nestling period. When the parents are able to provide their brood with plenty of food, the subordinate chick eventually catches up with its sib so that both chicks are similar in size and weight at fledging (Drummond et al., 1991). During periods of food shortage, however, subordinate chicks are more affected and more likely to die of starvation (Drummond et al., 1986). Hence, dominant status can be viewed as an indivisible resource for which both chicks could be expected to fight. Besides the obvious relevance of age and size differences in the establishment of dominance relationships, Drummond and Osorno (1992) have shown the importance of past experience of the chicks: when two unfamiliar, unrelated chicks are temporarily paired, each of them tends to adopt the role (aggressive or submissive) that it occupied in its home nest. If a small dominant chick is paired with a larger subordinate one from another nest, the formerly dominant chick is likely to re-establish its status (if the size and age asymmetry is not too large) and usually does so without much fighting (Drummond and Osorno, 1992). A similar effect of experience is found when studying the territorial behavior of juvenile steelhead trout (*Salmo gairdneri*, Abbott et al., 1985).

Game theoretical approaches to the evolution of contest behavior (e.g., Maynard Smith, 1982; Maynard Smith and Price, 1973) have shown that asymmetries in ownership (Maynard Smith, 1976), resource holding power (RHP, Parker, 1974), and payoff (Maynard Smith and Parker, 1976) may influence the behavior of contestants. Anecdotal evidence for the effect of payoff asymmetries comes from our observation (Kacelnik A, personal observation) that the dominance between two parent starlings (*Sturnus vulgaris*) at a feeding site can be reversed by manipulating their clutch size: on several occasions a previously subordinate individual became dominant when chicks were transferred from the previously dominant bird's nest to its own. Based on this kind of observation, Enquist and Leimar (1987) studied the expected evolutionary outcome of a sequential assessment game in which asymmetries in RHP and payoff are simultaneously present. They demonstrated that, at the evolutionarily stable strategy (ESS), if one player can benefit from the resource more than the other, it should be more eager to fight for it and more likely to obtain it, unless the difference in fighting ability opposes this outcome too strongly. Sequential assessment, however, is not essential for the derivation of this prediction. In the asymmetric war of attrition (Hammerstein and Parker, 1982; Parker and Rubenstein, 1981) contestants that benefit more from the resource are also more inclined to wait longer times, but because of the very nature of the war of attrition models, this tendency cannot be balanced by asymmetries in RHP. Hammerstein (1981) derived a "hawk-dove"-like game in which both payoff and RHP asymmetries were simultaneously present and concluded that both "Assessor" (if greater RHP escalate, else display) and "Bourgeois" (if expected payoff is large escalate, else display) strategies could be ESS for suitable parameter values.

We manipulated payoff asymmetry by food deprivation to study the effect of deprivation level on subsequent dominance status. We paired unacquainted chicks differing in level of food deprivation but similar in age and previous status (both were junior and, presumably, subordinate chicks). In order

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