Sibling bullying during infancy does not make wimpy adults

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Despite frequent suggestions that dominance–subordination relationships in infancy can affect subsequent agonistic potential during adult life, to our knowledge no explicit test has been made. Experiments have shown that adverse conditions during early development can have long-term effects on a variety of traits ranging from growth to competitive behaviour. In many vertebrate species, the main social setting in which the infant develops is a sibling group where competition is often mediated by a dominance hierarchy. Here, we show in a long-lived marine bird that subordination to an aggressive sibling throughout infancy does not compromise aggressiveness years later during adult life. Former junior and senior chicks of the blue-footed booby, whose typical brood of two chicks exhibits a consistent dominance–subordination relationship with strong ‘trained winner’ and ‘trained loser’ conditioning effects, did not differ in their aggressiveness while defending their nest against a conspecific intruder stimulus. Our results suggest that aggressive subordination and associated food deprivation, poor growth and elevated stress hormone during infancy do not prejudice aggressiveness of adult boobies during at least the first 13 years of life. Development of important traits such as aggressive tendencies may be buffered against the normal and predictable challenges of infancy.

Keywords: early development; siblings; dominance; aggressiveness; long-term

1. INTRODUCTION
Adverse conditions experienced during early development can play a key role in the life-history trajectories of organisms [1,2]. Experiments have shown that nutritional deficits during early development of vertebrates can prejudice growth, sexual attractiveness, immuno-competence, metabolic rate and competitive behaviour [1,2]. Even when poor nutrition is followed by compensatory growth, delayed costs can be expressed during adulthood [2], for example, in cognitive performance and dominance status [3,4]. Likewise, experimentally elevated circulating corticosterone in nesting birds can produce deficits in exploratory behaviour and competitiveness in adult life [5]. But does experience of aggression during early development, as aggressor or victim, affect an animal’s aggressive behaviour during adulthood?

Possibly, the most promising context for testing for such an effect is provided by the dominance relationships that mediate competition between infant broodmates and littermates (reviewed in [6]). It is frequently suggested that this sibling agonism affects competitive abilities and agonistic potential during adult life (e.g. [7–10]). Sibling relationships are often the main social setting in which the infant develops, and they can be sustained through a substantial part of early development, but no convincing test of their effects on agonistic behaviour during adulthood has been made in any species.

Here, we examined a long-lived marine bird for long-term or delayed effects of nesting dominance–subordination and its correlates on a social trait that is key to successful reproduction: aggressive nest defence. Two-chick broods of the blue-footed booby (Sula nebouxii) always develop an archetypical relationship of dominance–subordination in which, throughout the four-month nestling period, one chick (generally the elder) reliably pecks, bites and threatens while the other relies on submissive postures [11]. Detailed developmental analysis and experimental pairings of unfamiliar chicks have shown that these ‘trained winner’ and ‘trained loser’ roles are learned, persistent and powerful enough to prevail over large countering age/size inequalities [12]. But do trained winners outperform trained losers when it comes to defending territory, nest site and progeny against adult intruders several years later?

The booby’s dominance relationship confronts junior chicks with two additional developmental challenges [13]. First, during the first week of life, junior chicks receive fewer feeds and 17 per cent less fish from parents. This inequality continues thereafter and during the first three weeks of life junior chicks weigh 11 per cent less than senior chicks and exhibit a lower growth rate. However, between the fifth and tenth weeks, the growth of juniors exceeds that of seniors and by 70 days of age juniors are nearly as large and heavy as seniors. Second, levels of circulating corticosterone in junior chicks are 109 per cent higher than in senior chicks, at least between the ages of 15 and 20 days, probably owing to food deprivation. In addition, in an ‘El Niño’ year at least (under unfavourable environmental conditions), mothers deposited 10 per cent less yolk in second eggs than in first eggs, although the masses of first and second eggs did not differ [14]. Failure of former trained winners to outperform former trained losers in agonistic interactions during breeding would imply that aggressive subordination throughout infancy does not prejudice the development of adult aggressive behaviour, and further imply that neither do food deprivation followed by compensatory growth, elevated corticosterone or yolk deficit.

2. MATERIAL AND METHODS
(a) Study species
Throughout courtship, incubation and brood care, male and female blue-footed boobies singly and jointly defend a 7–20 m² patch of ground against neighbours and prospectors [15]. Defence involves ritualized handling of nest material, menaces, yes head-shakes, wing flaps and, occasionally, direct pecks and jabbing. Confrontations at territory boundaries during brood care pose a risk of territory loss, injury, damage to the brood and even infanticide ([11,16]; H. Drummond and O. Sánchez-Macouzet 1981–2010, personal observation).
but gender of the defending adult had a strong effect on the subjects' responses (between 15.00 and 18.00 h, with no effect of time of day on the aggression scores). Trials were run between 07.00 and 11.00 h and the observer remotely unmasked the stimulus and video-recorded aggression displays almost immediately. The stimulus was a stand-up, full frontal, life-sized, fibreboard-mounted colour photograph of a male adult intruder presented at a distance (90 cm from the subject) and location that mimicked a natural intrusion. After a 5 min delay for habituation, the stimulus was shown to the intruder stimulus with aggressive displays almost immediately, for up to 3.28 min. Trials were run between 07.00 and 11.00 h and between 15.00 and 18.00 h, with no effect of time of day on the subjects' responses (field significance of each term was assessed using likelihood ratio (GLM: status × age, status × age2 and status × hatch date) were fitted in an initial model, then non-significant interactions and main terms were dropped sequentially to simplify the model. The reported significance of each term was assessed using likelihood ratio (L-ratio) tests to compare the simplified minimal adequate model with the model including a non-significant term or with the model excluding a significant term (GLM: L-ratio1,72 = 11.921, p < 0.001), with males being twice as aggressive as females (males: 63.43 ± 7.96, females: 31.28 ± 5.27; figure 1).

Aggression scores were not significantly related to age, whether expressed as a linear term (GLM: L-ratio1,72 = 0.268, p = 0.60) or a quadratic term (GLM: L-ratio1,72 = 1.078, p = 0.30), and no difference in aggressiveness between former seniors and juniors emerged over the lifespan, at least up to age 13 years (GLM: status × age: L-ratio1,69 = 0.696, p = 0.40; figure 2).

Aggression was not significantly related to the subject's hatch date (GLM: L-ratio1,73 = 1.116, p = 0.29), body size index (GLM: L-ratio1,73 = 0.266, p = 0.61), brood size (GLM: L-ratio1,73 = 1.072, p = 0.30) or neighbourhood density (GLM: L-ratio1,73 = 2.779, p = 0.10), or to any of the interactions included in the initial model (in all tests, p > 0.47).

4. DISCUSSION

Contrary to expectation, former juniors of both sexes defended their nests against a conspecific intruder stimulus as aggressively as former seniors. Measures of adult aggression in other contexts, including escalated battles, could yet reveal a difference between former juniors and seniors, but our findings suggest that the aggressive competitive ability of junior boobies is not compromised, at least up to age 13 years, by aggressive subordination throughout infancy, nor by food deprivation and elevated corticosterone in the same period, nor by an earlier yolk deficit. Nor, apparently, is aggressive competitive ability enhanced at any age up to 13 years by growing up in the privileged circumstances of a dominant sibling. As far as we know, this is the first study of a vertebrate species in the

3. RESULTS

Former senior and junior chicks did not differ in their aggression scores (GLM: L-ratio1,71 = 0.045, p = 0.83; seniors: 45.12 ± 5.78, juniors: 50.18 ± 8.65; figure 1), but gender of the defending adult had a strong effect.
Aggressiveness of bullied siblings

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We thank A. Ramos, Y. Saldívar and S. Martínez for valuable assistance with fieldwork and observations. Logistical support was generously provided by C. Rodriguez, the fishermen of Nayarit, SEMARNAT and the Armada de Mexico, and finance by CONACYT (47599). We especially thank A. Núñez-de la Mora, C. Carmona-Isunza, M. Bekoff, D. Mock and an anonymous referee for comments on the manuscript.

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is unknown (reviewed in [13]). In the present study, competitiveness and other traits during adulthood have conditions during early development on dominance, the same aggressive potential in adulthood as seniors.

followed by compensatory growth and elevated circu-
sive subordination (combined with poor nutrition buffers them against an infancy of protracted aggressiveness in vertebrate infants, including those that grow of their broodmates, rather than to failure of intrinsically uncompetitive individuals. Importantly, the possibility of post-fledging sample bias can be discounted because annual survival and recruitment do not differ between former seniors and juniors at any age between fledging and 20 years [13,17].

Former juniors appear to be phenotypically equivalent to former seniors during adulthood: studies embracing the first 5–20 years of life have failed to detect inferiority in survivorship [13], body size and immune responsiveness of females [19] or any aspect of reproduction [17]. Importantly, former juniors and seniors do not differ in natal dispersal distance [20], indicating similar competitive abilities in the first 6 years of life. Natural selection may have favoured genotypes capable of coping with the adversity that many boobies predictably encounter during infancy. Apparently, the developmental programme of chicks buffers them against an infancy of protracted aggressive subordination (combined with poor nutrition followed by compensatory growth and elevated circulating corticosterone), and enables juniors to put their habitual submissiveness behind them and develop the same aggressive potential in adulthood as seniors.

Most studies documenting effects of adverse conditions during early development on dominance, competitiveness and other traits during adulthood have used experimental treatments whose ecological validity is unknown (reviewed in [13]). In the present study, adversity of the type, magnitude and timing naturally experienced by junior booby chicks did not affect their aggressive competitive ability later in adult life. In nature, the development of aggressiveness and competitiveness in vertebrate infants, including those that grow up in dominance hierarchies, may be more resilient to aggressive subordination and low status than biologists and psychologists usually assume.

Permissions for fieldwork were granted by SEMARNAT (SGPA/DGVS/00505/07).

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