

NON-BREEDING NAZCA BOOBIES (*SULA GRANTI*) SHOW SOCIAL AND SEXUAL INTEREST IN CHICKS: BEHAVIOURAL AND ECOLOGICAL ASPECTS

by

DAVID J. ANDERSON¹⁾, ELAINE T. PORTER and ELISE D. FERREE²⁾
(Dept. of Biology, Wake Forest University, Winston-Salem NC 29109-7325 USA)

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Summary

Adult Nazca boobies (*Sula granti*) show an unusual interest in both conspecific and congeneric nestlings, visiting them at their nest sites and performing mixtures of affiliative, aggressive, and sexual behaviours. Using a 20 year database from a large Nazca booby colony on Isla Española, Galápagos Islands, Ecuador, we describe the behaviour and the individuals performing the behaviour. Non-parental Adult Visitors ('NAV's') are typically 'unemployed' (non-breeding birds or recently failed breeders), and make visits of 1-60 min to unguarded chicks. Males and females are equally likely to exhibit the behaviour, if they are unemployed; since most unemployed birds are male, due to a sex ratio bias, most NAVs are male. Very young chicks and chicks nearing fledging are not visited, because young chicks are always attended by protective parents, and old chicks can defend themselves. When acting affiliatively, NAVs may simply stand by the chick, or may preen it and present gifts of pebbles and feathers. Aggression by the NAV often leaves scratches on the chick's body, but seldom causes the chick's death directly. However, landbirds take blood-meals from the scratches during food shortages, deepening the wound and eventually killing the chick. The least common NAV behaviour is sexual, in which adults perform male copulatory behaviour with the

¹⁾ Corresponding author's email address: da@wfu.edu

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chick. Sexual behaviour occurs in 14.3% of visits by males, and 6.8% of visits by females. NAV behaviour is the direct or indirect cause of mortality of up to 24.6% of chicks, representing up to 41.6% of all deaths, in a given year. Approximately 80% of non-breeding birds in a given year show NAV behaviour, and since most adults are non-breeders at some point in life, most adults show NAV behaviour at some point. We propose a number of hypotheses to explain the causation of this puzzling and ecologically important behaviour.

Keywords: sexual behaviour, seabird, infanticide, booby, *Sula*.

Introduction

Most behavioural interactions between adult animals and conspecific young fall into two general categories: affiliative and aggressive. Parents provide care to their own offspring in affiliative relationships, and in some circumstances parental and non-parental adults provide care to other more distantly related offspring (communal suckling in lions, Pusey & Packer, 1994; worker ant care of siblings, reviewed by Bourke, 1997; cooperative breeding in birds, Curry, 1988; Emlen & Wrege, 1988). Also, young sometimes have play relationships with adults in highly social species (*e.g.* in primates, Singh, 1986). In the realm of aggressive interactions, parents may attack young from outside their family to prevent those young from stealing parental care from the family (in colonial gulls, Fetterolf, 1983; reviewed by Pierotti, 1991), or parents may practice adaptive infanticide within their family as a mechanism of brood reduction (in coots, Horsfall, 1984; reviewed by Stanback & Koenig, 1992). Adults often kill the young of another animal to acquire that adult as a mate or to take over a nest site (in female Belding's ground squirrels, Sherman, 1981; tree swallows, Robertson & Stutchbury, 1988; little swifts, Hotta, 1994; and male lions, Packer *et al.*, 1990). Adults may also kill young to eliminate competitors for other kinds of resources, such as food (in primates, Agoramorthy & Rudran, 1995). Parents and/or unrelated adults may cannibalize young as a food source (in falcons, Bortolotti *et al.*, 1991; fish, Lissaker *et al.*, 2003; heteroptera, Thomas & Manica, 2003). Finally, in some cases infanticide appears to have no adaptive basis, or occurs under stressful situations, and may be viewed as a maladaptive social pathology (reviewed by Hrdy, 1979).

When adults actively seek out conspecific young with which to interact (outside the context of parental care), the young are usually killed during the interaction. A notable exception is that of pedophilia in humans, in which

adults have a sexual, and not necessarily lethal, interest in young. Similar behaviour is virtually unknown in non-human wild animals, although it has been reported from captives (de Waal, 1987) and anecdotally from some wild populations (*e.g.* avian species in which the posture of chicks resembles that of sexually active females, Besnard *et al.*, 2002; Ewen & Armstrong, 2002). Adult Nazca boobies (*Sula granti*; American Ornithologists Union, 2000), ground-nesting colonial seabirds in the family Sulidae, provide a rare example of frequent sexual interest in young, approaching partly grown chicks whose parents are absent and engaging in mixtures of sexual, aggressive, and affiliative behaviour (Nelson, 1978, p. 411 and Figure 157(b); Tarlow *et al.*, 2003). The behaviour is not simply territorial defense, and is not restricted to conspecifics: adults will travel into non-habitat (the rocky intertidal zone) in a highly directed manner to reach blue-footed booby (*S. nebouxii*) chicks placed there experimentally (Townsend *et al.*, 2002). Similar behaviour is known from pelicans, a related family (Schaller, 1964; Brown & Urban, 1969; Din & Eltringham, 1974).

The causation of this behaviour is of interest in several respects. It is rare among animals, yet has elements in common with human behaviour. Additionally, the interactions between chicks and their Non-Parental Adult Visitors (NAV) frequently result in lacerations on the chick's body, leading indirectly to the chick's death via ectoparasitic blood-feeding by landbirds (Curry & Anderson, 1987), so NAV behaviour represents a potentially important ecological effect on breeding. Finally, we have a developing understanding of the hormonal characteristics of NAVs (Tarlow *et al.*, 2003), linking it to the field of behavioural endocrinology. Our study site in the Galápagos Islands contains large numbers of densely nesting birds, which tolerate close human presence that facilitates behavioral observation.

Here we place the NAV phenomenon in behavioural and ecological contexts and generate hypotheses for the causation of the behaviour. We characterize the behaviour itself, and the adults performing NAV behaviour, using 20 years of data from the study population. We also document the reproductive consequences of NAV-induced mortality. Since landbird blood-feeding ultimately causes the mortality, we reasoned that variation in landbird food availability could explain inter-year variation in NAV-induced mortality. Accordingly, we examined the relationship between the timing of the seasonal rains (causing a flush of food) and the incidence of NAV-induced death by blood-feeding.

Materials and methods

We studied Nazca booby nesting biology at Punta Cevallos, Isla Española, Galápagos Islands (1°23'S, 89°37'W), Ecuador between 1984 and 2003 in conjunction with other long-term research on this species. Anderson & Ricklefs (1987) and Huyvaert & Anderson (2004) provide details of the study site. Approximately 3500 Nazca booby pairs breed at Punta Cevallos (Anderson, 1993), with eggs laid from October to February and fledging occurring from March until June. Breeding seasons thus span parts of more than one calendar year, and are referred to by the first year of the span (*e.g.* the '1995 season' is the 1995-96 breeding season).

We began ringing adult and chick Nazca boobies in the 1984 season with numbered metal rings to enable identification of birds. Ages of birds ringed as chicks are known exactly; birds ringed as adults can be assigned a minimum age only, based on the date of ringing and the earliest age at which birds are typically seen as adults in the colony (4 yr; Huyvaert & Anderson, 2004). The age structure during the 2002 season provided many known-age birds of less than 10 yr, and many known-age and minimum-age birds of 10 yr or older. Age-specific analyses of the 2002 data thus categorized birds as <10 yr or \geq 10 yr, to maximize sample sizes of age groups.

We monitored the breeding of all ringed birds annually in all three subcolonies of the Punta Cevallos study site (sub-colonies 1-3 in Huyvaert & Anderson, 2004). Beginning with the 1984 season, all researchers in our group have watched for NAV events while working in the study site, and have recorded the behaviours performed, the NAV's ring number (if any) and sex, the chick's nest or ring number, and other details. We also have watched for and recorded landbirds taking blood meals from wounds on chicks (Curry & Anderson, 1987). These *ad lib.* observations were used to characterize general elements of NAV behaviour and to identify which times of year, and under which ecological conditions, landbirds blood-feed.

In one small area of approximately 450 nests in subcolony 1 (Huyvaert & Anderson, 2004) we monitored breeding of all ringed and unringed birds annually. This entire 'Study Area' was systematically patrolled during the afternoon hours by one or more observers during the 1998, 2000, 2001, and 2002 breeding seasons, attempting to record all NAV events that occurred. Data from these years were detailed with respect to the ages of all chicks involved, the identities of the NAVs, and which behaviours were performed. Finally, in the 2002 season, we performed two series of ringings with numbered plastic leg rings that could be read easily from a distance. We ringed all non-breeders and failed-breeders (collectively referred to as 'unemployed' birds) in the Study Area prior to commencement of any NAV activity that season. These birds were then monitored by daily and nightly ring recapture surveys, and 'residents' of the colony were determined based on the number of presences per bird. Additionally, approximately 30% of the Study Area was designated as the 'Mini-area', in which all breeders also wore plastic leg rings. Birds in the Mini-area were used for time budget studies in the 2002 season, by visiting each nest hourly from 0600-1800h, and additionally at 0530h (sunrise) and 1830h (sunset) to record which parents were present. From these time budget data we determined the number of daylight hours per day that chicks of different ages were left unattended by their parents. The high density of birds in the colony at night apparently precludes the movement around the colony that NAVs require to find unattended chicks: in over 1000 person-hours of nighttime work at the study site, we have never seen a NAV event.

From detailed field notes we classified all NAV behaviours into three categories. 'Affiliative' behaviours included simply attending a chick, preening, gently touching, and presenting

gifts (twigs, feathers, pebbles). These behaviours are typical of normal parent-offspring and pair-bond interactions (Nelson, 1978). 'Aggressive' behaviours included biting or jabbing the chick's body (usually the neck, base of the skull, wing, or rump), clamping and shaking vigorously, and pulling on the chick's down. 'Sexual' behaviours were restricted to copulation attempts, in which the NAV stood on the chick's back, treaded alternately with the feet, and made pre-copulatory or actual copulatory movements of the tail.

Daily rainfall accumulation was recorded each day at 0700h. The 1989 season was unusual in that Darwin's finches (*Geospiza sp.*) showed high rates of starvation and took blood meals from booby chicks. We measured food abundance using the sampling scheme of Schluter & Grant (1984), in which all seeds and fruits found in and above randomly-placed 1 m² quadrats were collected and identified in January 1990. The edible (non-toxic) items were summed for each site; edible items were in the genera *Panicum*, *Boerhaavia*, *Alternanthera*, *Lantana*, *Blainvillea*, *Cenchrus*, *Prosopis*, *Portulaca*, *Cordia*, *Aristida*, and *Rynchosia*. DJA participated in the October 1981 sampling on Española reported in Schluter and Grant (1984) and provided consistency in methodology. The 1981 sampling was done with 0.125 m² quadrats; 1 m² quadrats were used in the January 1990 sampling to increase resolution because seed densities were low.

For each of the systematic NAV observation years (1998, 2000, 2001, 2002) we calculated the percentage of chick deaths (excluding siblicidal mortality, Anderson, 1989) that could ultimately be attributed to 1) NAV-induced injuries, exclusive of subsequent blood-feeding, 2) blood-feeding from NAV-induced injuries, 3) a combination of starvation and weakening by NAV visits, and 4) other various causes, such as starvation alone or depredation by Galápagos hawks (*Buteo galapagoensis*), or for unknown reasons. Statistical analyses were performed with Statistica v5.5 (Statsoft Inc., 1999). Parametric statistical tests were used when appropriate assumptions were met; when necessary, nonparametric alternatives were used. Statistical significance was set at $\alpha = 0.05$, and significance tests were two-tailed.

Results

Description of NAV behaviour

We recorded a total of 4,945 NAV events in the 1984-2002 seasons. The majority of these (3,793) involved only a single NAV (2,303 males, 279 females, and 1,211 of unknown sex), while 1,799 involved two adults (male/female couples, with the exception of six male/male couples). Five events involved mixed-sex trios. In all events, the NAV approached the chick (or the chick and one or more NAVs) in a directed manner across the flat, open terrain of the breeding colony, typically walking rapidly and gazing fixedly at the target chick; NAVs did not simply blunder onto chicks, and chicks did not approach NAVs.

We recorded the behaviours performed in 3,544 of these NAV events. Males participated in 2,614 of these events, showing either a single behaviour type (1309 events: 50.1%) or a mixture of types (1305 events: 49.1%).

TABLE 1. *Numbers of NAV events in which each of three behaviour types were recorded for males and females*

	Aggressive	Affiliative	Sexual
Males	1426 (0.546)	813 (0.311)	375 (0.143)
Females	556 (0.598)	311 (0.334)	63 (0.068)

Row totals exceed the total number of events because more than one behaviour type was recorded for some events. Proportions in parentheses are number of events for each behaviour type divided by the total number of events for that sex, representing the proportion of events in which that behaviour was recorded for that sex.

Females participated in 930 of these events, 492 (52.9%) showing a single type, and 438 (47.1%) showing a mixture. Males and females showed similar distributions of behaviour types, with aggression the most common behaviour, followed by affiliative and sexual behaviours (Table 1). Nonetheless, the frequencies in Table 1 showed significant heterogeneity ($G = 40.53$, $df = 2$, $p < 10^{-6}$), indicating that males and females differed in their tendencies to exhibit the different behaviours. The sexual behaviour of females toward chicks was indistinguishable from male-type copulatory behaviour. As far as we could tell, the chick's prone posture prevented the NAV from making cloacal contact, and we never observed ejaculation during copulation, nor did we find ejaculate on the chick after NAV events.

For 1,116 events involving aggression, the level of aggression was coded as moderate or high. During moderate aggression, NAVs bit but did not shake the chick, whereas high aggression involved both biting and shaking, and creation of visible wounds. Female NAVs were more likely to exhibit the high level (24.6% of 187 events) than males were (16.8% of 929 events; $\chi^2 = 6.40$, $df = 1$, $p = 0.011$).

During part of the 2000 season we observed all events from detection until completion. Durations of these 248 events ranged from 1-60 min, but the majority (84.7%) lasted 10 min or less (median = 3 min). Males and females did not differ in the durations of their events (Mann-Whitney $U = 4877$, $N_1 = 162$, $N_2 = 66$, $Z = 1.038$, $p = 0.30$).

During the 2000 season we recorded any interactions between a NAV and another non-parental adult. During 240 events a single NAV was approached by another non-parental adult. In 67 of these events (27.9%) the second bird was of the other sex and joined the first at the chick's nest. In the remaining 173 events (72.1%) repulsion occurred, in the form of fighting or chasing,

and only one of the two birds remained at the chick's nest. For repulsions in which the sex of both adults is known, the majority were performed by males toward other males ($56/77 = 72.7\%$), though occasionally males and females repelled a bird of the opposite sex.

Without exception, NAV events began only when the visited chick's parents were absent. On the rare occasions when a parent returned to its nest while a NAV was present, the NAV immediately fled the nest site, escaping advancing attack by the parent. Since NAV events occurred during parental absence and parents tended to be absent in the afternoons (Anderson & Ricklefs, 1992), most NAV events occurred during the afternoon (Fig. 1). As chicks grew, parents tended to spend more time away from the nest (Anderson & Ricklefs, 1992), so older chicks presented more opportunities for visits (Fig. 2A). However, chicks of asymptotic body size (Fig. 2B) were able to repel NAVs (Porter, 2003) so visits were made to chicks old enough to be unattended but not large enough to defend themselves. The NAVs' selection of medium-age chicks was especially apparent in mid-March, 2003, when excellent breeding conditions produced an unusually large number of late-stage chicks, which were visited infrequently (Fig. 2C). As a result, most visits were made to chicks 30-80 days of age (Fig. 2D). For developmental

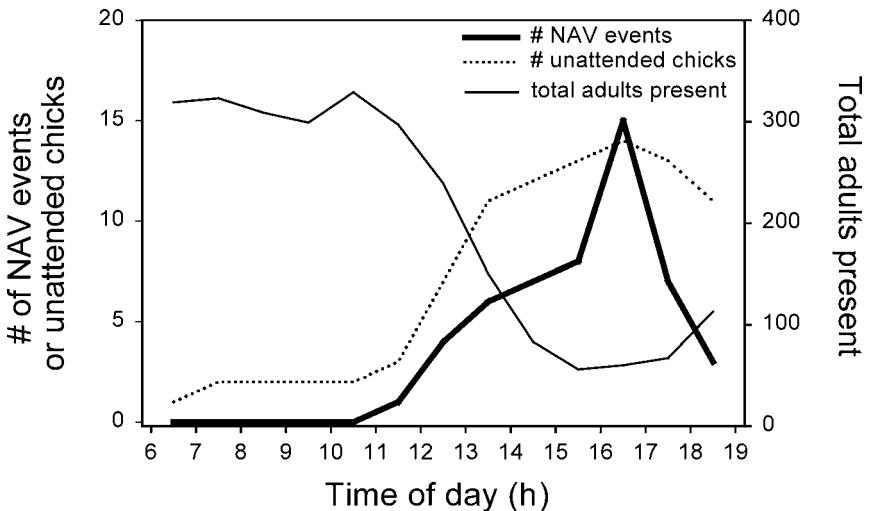


Fig. 1. Time course of total adult attendance, number of unattended chicks, and number of NAV events during daylight hours of a typical day in the Study Area (April 8, 1986).

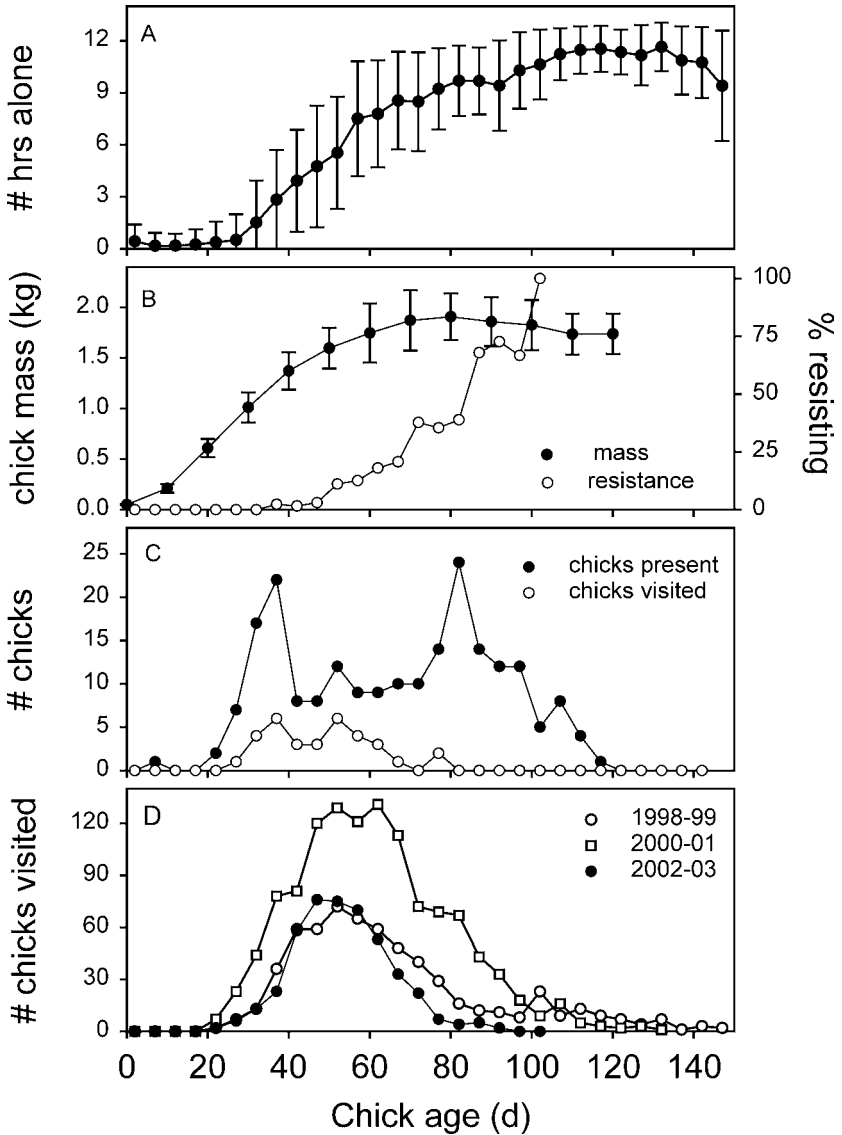


Fig. 2. A: number of hours chicks spent alone (mean \pm SD) as a function of chick age in the Mini-Area during the 2002 breeding season ($N = 63$). B: chick mass (mean \pm SD) and chick defensive resistance of approaching NAVs as a function of chick age in the Mini-Area during the 2002 breeding season ($N = 63$). C: age structure of the chick population, and ages of chicks visited by NAVs, in the Study Area on 15-16 March 2003. D: ages of all chicks visited by NAVs during three breeding seasons.

context, most chicks attain juvenile plumage at 90-110 days of age, and fly competently for the first time around 120 days (Nelson, 1978).

During the 2000 season we recorded any aggression directed toward NAVs during a visit to a chick. Of 1,655 events in that season, a parent returned to the nest during 26 (1.6%) of them and drove off the NAV, but without significant physical contact. NAVs fought with nearby adults in 34 (2.1%) of these events, and within-pair fights of NAVs occurred in 5 (0.3%) events. In 19 (1.2%) events, the chick aggressively defended itself against the NAV. No NAV appeared to be injured in any of these cases, and only 5.2% of events involved the potential for injury due to aggression.

Characteristics of NAVs

Log-linear analysis showed significant associations between behaving as a NAV at least once during the 2002 season and both breeding status ($\chi^2 = 296.66$, $df = 1$, $p < 10^{-6}$) and sex ($\chi^2 = 8.72$, $df = 1$, $p = 0.003$): unemployed birds, but not current breeders, were likely to perform NAV behavior, and male NAVs were more often non-breeders and female NAVs were more often failed breeders (Fig. 3). Most of the few successful breeders recorded as NAVs interacted aggressively with neighboring chicks; however, three successful breeders interacted with chicks in other parts of the colony when their

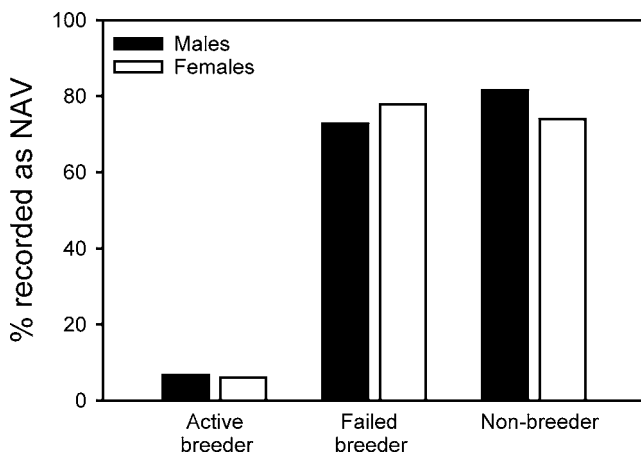


Fig. 3. Percentage of successful breeder, failed breeder, and non-breeding adults (405 males, 244 females) recorded as NAVs in the Mini-Area during the 2002 breeding season.

own chicks were approaching fledging age. Failed breeders showed NAV behaviour only after their breeding attempt failed (45/51; 88.2%) or while they were intermittently incubating failed eggs past the expected time of hatching (6/51; 11.8%). The mean time between breeding failure and the first NAV event for a failed breeder was 15.3 d (SD = 14.3).

In 2002, ages were known for 240 of the resident unemployed birds. Log-linear analysis of age, sex, breeding status (non-breeder or failed breeder), and whether recorded as a NAV detected a significant association of NAV behaviour with age class ($\chi^2 = 12.92$, $df = 1$, $p < 10^{-3}$); 88.5% of birds less than 10 yr old engaged in one or more NAV events, while 68.1% of birds 10 yr and older did. No other two-way interaction was significant, but we did note a single significant three-way interaction, of sex, breeding status, and probability of showing NAV behaviour ($\chi^2 = 4.34$, $df = 1$, $p = 0.037$).

Considering all 117 NAVs recorded during the 1998 breeding season that survived until the 2002 breeding season, 54/85 males (63.5%) and 27/32 females (84.4%) attempted to breed at least once during the four breeding seasons subsequent to the 1998 season.

Chick behaviour

Although it is not the focus of this paper, the behaviour of visited chicks is relevant to the interpretation of NAV behaviour. Chicks usually adopted the submissive 'pelican posture' (Nelson, 1978) as a NAV approached, prone on the ground with the dorsal surface of the bill pressed against the ground and tucked under the body, and appendages held tightly against the body. As the NAV moved to different parts of the nest site, many chicks tilted their heads to present the back of the head to the NAV, thereby concealing the bill from the NAV's view. Despite the submissiveness of the chick's posture, NAVs regularly bit the exposed neck, wings, and rump of the chick. Lifting the bill from the substrate appeared to release aggression by the NAV; chicks nonetheless raised the bill sometimes to thermoregulate by gular flutter (Bartholomew, 1966), thus inducing further attacks. The curved neck presented in the pelican posture was the part of the chick most frequently bitten by NAVs. In the case of a NAV behaving exclusively affiliatively, chicks occasionally assumed an upright stance and interacted with the NAV as parent and chick normally interact, except that we have never observed food exchange between NAV and chick. Finally, older chicks used aggressive displays such as wing-flailing, yes-no head-shaking, jabbing, and vocalizations

(Nelson, 1978) to repel approaching NAVs. Most chicks that reach at least 21 days of age are visited at least once (1998: 92/114 = 80.7%; 2000: 172/191 = 90.1%; 2001: 111/160 = 69.4%; 2002: 205/221 = 92.8%).

NAV-induced chick mortality and landbird ecology

The signature of a NAV's visit is paired patches of scratched skin and missing down on a chick's neck, due to the NAV's repeated clamping of the chick's neck. While most chicks older than 60 days show this evidence of visits, the frequency and severity of visits and the associated probability of mortality decline as chicks age past this point. Not only do a greater proportion of older chicks resist the approach of a NAV (Fig. 2B), but also the proportion of defensive chick acts that result in retreat of the NAV increases with chick age (Porter, 2003). By 90 days of age most chicks resist the approach of a NAV (Porter, 2003) and are successful at repelling the NAV in this way.

Injuries inflicted by NAVs seldom caused chick mortality, but these injuries frequently led indirectly to a chick's death via landbird blood-feeding (Fig. 4). The mortality rate due to blood-feeding and to all NAV-induced causes varied considerably between years (Fig. 4). Few chicks died from the combined effects of NAV injuries and starvation, because most badly injured chicks died from blood-feeding before starvation.

Galápagos mockingbirds (*Nesomimus macdonaldi*) perched on the chick, or on the substrate near the chick, and pecked at fresh wounds, but never initiated wounds themselves. After several hours of such pecking, the hole often penetrated the skin and sub-dermal muscle layer. Mockingbirds inserted their long decurved bills into the hole, drinking blood and removing small pieces of tissue. Chicks were increasingly traumatized by the blood-feeding as the hole deepened, and generally died 24-48 h after blood-feeding began, often wandering aimlessly around the colony and dying far from their nest.

Landbird blood-feeding activity showed a correspondence with the pattern of rainfall and subsequent food availability: blood-feeding typically stopped following a two-week accumulation of 50 mm of rain (Fig. 5), because landbirds basically vacated the colony. In several years we observed no blood-feeding, either because more than 50 mm in two weeks fell unusually early when injured chicks were not yet available (1994, 1997, 1999), providing a sufficient stimulus to leave the colony, or because few chicks were produced in that season (1999). In three seasons (1996, 1998, 2002), blood-feeding continued throughout the chick population's window of vulnerability because little rain fell during the window.

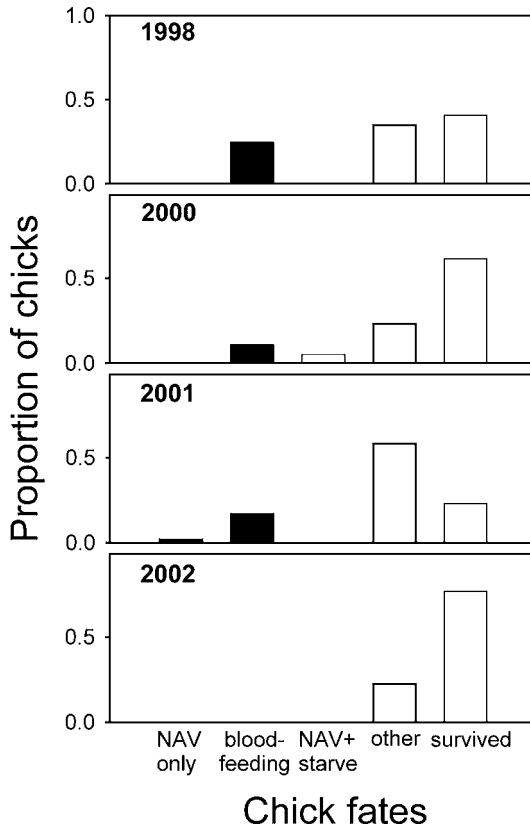


Fig. 4. Number of chicks surviving until attaining juvenile plumage and number of deaths ultimately caused directly by NAV attack only, indirectly by NAV attacks via blood-feeding, by a combination of starvation and NAV-inflicted injuries, or by other factors, for each season of systematic NAV observation in the Study Area. Year refers to the year in which each breeding season began.

Most blood-feeding was done by mockingbirds, but in two years (1990 and 2001), large cactus ground finches (*Geospiza conirostris*) also took blood meals. These finches were in poor plumage condition and of generally low vigor during the period in which blood-feeding was observed, implicating food shortage in their unusual switch to blood meals. In January 1991, density of edible seeds at Punta Cevallos in 20 plots (median = 0.5 seeds/m², range 0-5) was approximately 1% of that at 20 comparable coastal sites near Punta Cevallos sampled in October 1981 (median = 48 seeds/m², range 0-1774; Mann-Whitney $U = 45$, $Z = 4.17$, $N_1 = N_2 = 20$, $p < 10^{-4}$).

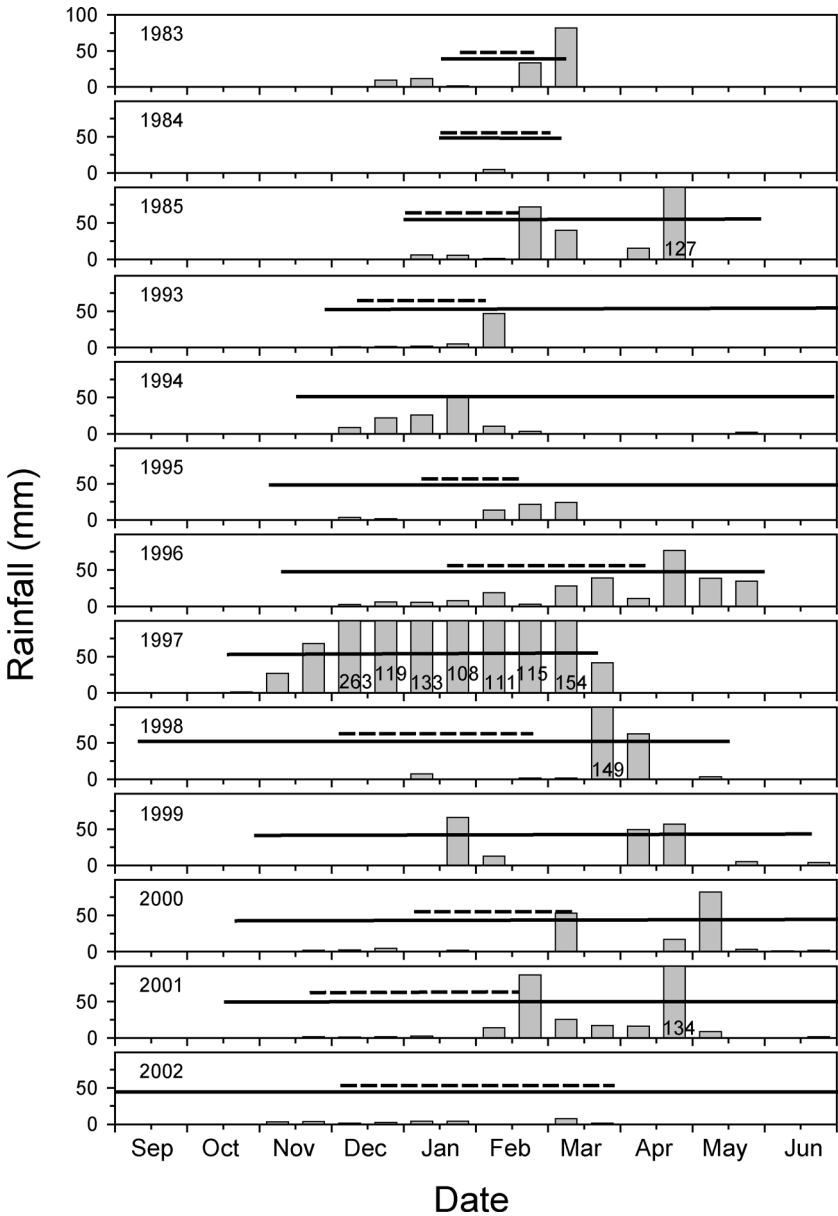


Fig. 5. Rainfall (bars), presence of investigators at the research site (solid horizontal line), and records of landbird blood-feeding (dashed horizontal line), grouped in half-month periods. Rainfall totals greater than 100 mm are printed on the relevant bar. Year refers to the year in which each breeding season began.

Compounding the food shortage was the fact that all of the seeds recorded in January 1991 were of *Cordia lutea*, a large hard seed that is difficult to crack (Grant, 1999). Most of the *Cordia* seeds that we recorded already had bite marks on them, indicating that a large cactus ground finch (the largest finch on Española), had already tried unsuccessfully to crack them.

Discussion

Non-breeding adult Nazca boobies are attracted to both conspecific and congeneric nestlings (Townsend *et al.*, 2002), joining them at their nest sites and directing various affiliative, aggressive, and sexual behaviours toward the nestling. Most NAV events involve aggression toward the chick. Approximately half of all events include some affiliative behaviour, and some visits include copulation attempts with the chick (Table 1). The visits may last for hours, but typically end within 10 min. The only qualities that we have identified that predict an adult's likelihood to perform NAV behaviour are breeding status and age: most unemployed birds that are present in the breeding colony engage in NAV behaviour, and birds less than 10 yr old are more likely to show NAV behaviour than are birds 10 yr old or older. Non-breeders (who did not attempt to breed in a given year) and failed breeders have similar probabilities of visiting chicks (Fig. 3). Birds with an active breeding effort very rarely visit chicks in other nests; conversely, unemployed males and females are equally likely to exhibit NAV behaviours, and most do so. However, more NAV events involve males than females because the male-biased operational sex ratio of this population (Townsend & Anderson unpubl. results) leaves more males than females unemployed. Likewise, more NAV events involve young than old birds, largely because younger birds are more likely to be unemployed because they have not yet begun to breed or because they attempted to breed and failed. Thus, most NAVs are young, unemployed males, and they make most visits in the mid- to late afternoon (Fig. 1).

A number of hypotheses could illuminate the causation of NAV behaviour. If the behaviour had no adaptive basis, or was maladaptive, it could be termed a social pathology, and perhaps could be attributed to peculiarities of some individuals, some periods of time, or some breeding colonies. However, NAV behaviour is apparently a normal part of Nazca booby life at Punta Cevallos, and is not specific to that colony: on two other Galápagos islands, we have

seen either NAV behaviour (I. Daphne) or many chicks with the characteristic neck scrapings (I. Genovesa, unpub. data). Given the high probability that an unemployed adult will engage in the behaviour (Fig. 3), the deferred age of first breeding (Huyvaert, 1999) and frequent breeding failures (Fig. 4), most adults at Punta Cevallos probably act as a NAV at some point in their lives. Furthermore, birds that attempt to breed and fail typically become NAVs in that same year, and birds acting as NAVs in one year typically attempt to breed in a subsequent year, if they survive. Thus, NAVs are not an unusual subpopulation with a permanently disturbed behavioural repertoire. Instead, the NAV behavioural state appears to be an alternative state to that of breeding, and individuals switch between states during their adult lives. This widespread nature of the behaviour must be accounted for by any hypothesis invoking non-adaptive causation.

At the ultimate level, the extensive literature on infanticide indicates that aggression toward chicks might enhance a NAV's fitness in several ways, including acquisition of a mate or nest site if the chick's injuries or death cause the divorce or nest site abandonment of the chick's parents (*e.g.* Sherman, 1981; Robertson & Stutchbury, 1988; Hotta, 1994; Packer *et al.*, 1990). In these cases, NAV behaviour evolves as an adaptation to manipulate the future actions of other adults by harming their present chick. Likewise, NAV behaviour that induces chick mortality could eliminate future competitors for mates (if same-sex chicks are targeted; Christenson & Le Boeuf, 1978; Sherman, 1981) or resources. NAVs seldom act aggressively enough to ensure the chick's death, so the behaviour may appear to fail to meet the *a priori* design specifications that many would look for (Williams, 1992; Lauder, 1996) in the putative adaptation of these hypotheses: it is not infanticidal, it is frequently not aggressive, and it frequently includes affiliative and sexual elements that do not obviously harm the chick (Table 1). A broader view recognizes that non-lethal and subtle harm to chicks could have a negative influence on the chick's fitness, and so perform the function embodied in these hypotheses, but the notable existence of affiliative behavior by NAVs would still remain problematic.

NAV behaviour may be an epiphenomenon of positive selection on some other trait, and is under weaker negative selection itself. For example, it may represent cases of mistaken identity, in which nestlings stimulate the same social response as a prospective mate; however, the aggressive nature of most visits calls this hypothesis into question. The pairing of an unusual

adult behaviour (that of NAVs) and an unusual nestling behaviour (obligate siblicide; Anderson, 1989) in this species suggests an organizational effect linking perturbations in neonatal corticosterone, progesterone (Tarlow *et al.*, 2001), and especially testosterone (Ferree *et al.*, in press) levels during siblicidal attacks and hormonal peculiarities (elevated corticosterone and lower testosterone) associated with the affiliative, aggressive, and sexual interest of adults later in life (Tarlow *et al.*, 2003). While selection for siblicidal behaviour by nestlings appears to be strong (Anderson *et al.*, unpub. data), selection against NAV behaviour, in terms of injuries during visits, appears to be weak (although the importance of elevated corticosterone in NAVs remains to be evaluated). Under this organizational effects hypothesis, we would expect adults that were siblicidal as nestlings to be most likely to perform NAV behavior as adults.

Injuries inflicted by NAVs can lead indirectly to the chick's death via landbird blood-feeding, which appears to be strongly food-related. During the annual dry season, food for landbirds becomes increasingly scarce, and seabird chicks become an increasingly attractive option. Darwin's finches were recorded taking blood meals in only two seasons, and for one of those we presented direct evidence of severe food shortage, so blood meals appear to be a foodstuff of last resort for finches. Blood-feeding is rare among birds, although another Darwin's finch species (*Geospiza difficilis*, Grant, 1999), and oxpeckers (*Buphagus erythrorhynchus*, Weeks, 1999), are known to drink vertebrate blood at least occasionally. Blood presents a metabolic challenge to birds due to the imbalance of the amino acids leucine and isoleucine relative to the ratio in proteins assembled by the bird ('amino acid antagonism'; Harper *et al.*, 1970; Calvert *et al.*, 1982). While relatively small amounts of nutritionally balanced foodstuffs should in theory alleviate this problem, blood-feeding at our site occurs when other landbird foods are hardly available, perhaps contributing to the finch's avoidance of blood except during extreme food shortages. Finches may be less likely than mockingbirds to take blood meals because they are less omnivorous than mockingbirds are (Grant, 1999). Mockingbirds took blood meals avidly in most years, and so posed a more consistent hazard to Nazca booby chicks. However, this hazard was closely tied to the timing of rainfall, and mockingbirds abandoned blood-feeding immediately after a threshold amount of rain fell (Fig. 5).

NAVs visit chicks of a characteristic age. Visited chicks are old enough that their demand for food requires their parents to leave them unguarded for some part of the day; this window of vulnerability for chicks begins at approximately age 20 d (Fig. 1). The visits stop when chicks reach a size and level of motor coordination that permits them to successfully repel NAVs, at approximately age 70 d (Fig. 1). During the window of vulnerability, most chicks are visited at least once, and if a chick's window opens before the first heavy rains of the season, then the risk of mortality via blood-feeding exists (Fig. 5). This circumstance has a number of implications for the timing of breeding and time budgets of parents. For example, hatching eggs in March rather than October would usually move the entire window of vulnerability after the seasonal rains fall (usually January-April; Grant, 1999). Nonetheless, most hatching occurs from October-January (Anderson, 1993), thus exposing most chicks to a high risk of blood-feeding. Given that this risk exists, parents apparently face a tradeoff between guarding a mid-sized chick from NAVs and meeting its food demands, implicating this unusual behavior in the evolution of the reproductive life history of Nazca boobies.

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