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Source: The Auk, 128(4) : 615-619

Published By: American Ornithological Society

URL: https://doi.org/10.1525/auk.2011.11008

The Auk
An International Journal of Ornithology
Vol. 128 No. 4 October 2011

The Auk 128(4):615–619, 2011

RAPID COMMUNICATIONS

MALTREATED NESTLINGS EXHIBIT CORRELATED MALTREATMENT AS ADULTS: EVIDENCE OF A "CYCLE OF VIOLENCE" IN NAZCA BOOBIES (*SULA GRANTI*)

Martina S. Müller, Elaine T. Porter, Jacquelyn K. Grace, Jill A. Awkerman, Kevin T. Birchler, Alex R. Gunderson, Eric G. Schneider, Mark A. Westbrock, and David J. Anderson[1]

Department of Biology, Wake Forest University, Winston-Salem, North Carolina 27109, USA

Abstract.—The "cycle of violence" hypothesis implicates child abuse as a cause of later violent behavior via social transmission between generations. It has received mixed support from human research and has prompted the study of nonhuman models with comparable abuse behaviors. The underlying biology of child abuse remains a controversial subject, perhaps partly because in nonhuman animals similar behavior occurs relatively rarely in wild populations. The Nazca Booby (*Sula granti*), a colonial seabird, provides a nonhuman model in which maltreatment of nonfamilial young is widespread under normal living conditions. Essentially all adults show social attraction at some point in their lives to the offspring of other parents, often with a sexual and/or aggressive motivation. Here, we show a correlation between the degree to which a young bird is targeted by such adults and its own infliction of maltreatment later in life. The results provide the first evidence from a nonhuman of socially transmitted maltreatment directed toward unrelated young in the wild. *Received 10 January 2011, accepted 15 June 2011.*

Key words: child abuse, developmental trauma, organizational effect, personality.

Los Pichones Maltratados Exhiben Maltrato como Adultos: Evidencia de un "Ciclo de Violencia" en *Sula granti*

Resumen.—La hipótesis del "ciclo de violencia" implica que los malos tratos a los menores son una causa de comportamiento violento posterior vía transmisión social entre generaciones. Esta hipótesis ha sido parcialmente apoyada por investigación en humanos y ha promovido el estudio de modelos no humanos con comportamientos abusivos comparables. La biología subyacente del maltrato a los menores sigue siendo un tema controvertido, debido tal vez en parte a que en animales no humanos un comportamiento similar aparece poco frecuentemente en poblaciones silvestres. *Sula granti*, una especie de ave marina colonial, constituye un modelo no humano en el cual el maltrato de jóvenes no emparentados es común bajo las condiciones normales de vida. Esencialmente todos los adultos muestran una atracción social en algún punto de sus vidas hacia los pichones de otros padres, usualmente con una motivación sexual y/o agresiva. Aquí, demostramos una correlación entre el grado al cual un joven es hostigado por tales adultos y su propio maltrato a otros individuos más tarde en la vida. Los resultados brindan la primera evidencia en una especie no humana de maltrato transmitido socialmente direccionado hacia jóvenes no emparentados en estado silvestre.

According to the "cycle of violence" hypothesis, traumatic abuse or neglect of developing young predisposes the maltreated individuals to exhibit the same maltreatment as adults.[1] The vast majority of the literature on this topic covers the human situation or captive nonhuman mammals.[2,3] We are aware of no studies of intergenerational transmission of maltreatment behavior in birds. However, colonial

[1]Address correspondence to this author. E-mail: da@wfu.edu

The Auk, Vol. 128, Number 4, pages 615–619. ISSN 0004-8038, electronic ISSN 1938-4254. DOI: 10.1525/auk.2011.11008

bird species provide an important opportunity to test the cycle of violence model because nestlings experience aggressive and even sexual maltreatment from adults and larger nestlings.[4–6] These nestlings can often be recognized later in life by leg bands or other identifiers, allowing study of their own adult social behaviors. We tested the cycle of violence hypothesis in a colonial seabird, the Nazca Booby (*Sula granti*), a species in which nestlings regularly experience abusive visits from nonfamilial adults,[4] and which show high natal philopatry.[7] We documented the exposure of nestlings to these visits, and then years later evaluated their behavior as adults in the same colony.

Nazca Boobies raise solitary nestlings on the ground in dense colonies, and frequently leave their offspring unattended while foraging for them at sea. During that time, nonbreeding adults (i.e., those that had not attempted to breed or had tried and failed) seek out unguarded nestlings for social interaction.[4] These nonparental adult visitors (NAVs) express a suite of behaviors dominated by aggression but also including affiliative and sexual acts, and virtually all nestlings experience at least one interaction.[4,8] Both males and females show all types of NAV behavior, including male-typical copulatory behavior. Siblicidal behavior at hatching reduces 2-chick broods to 1-chick[9] and is associated later in life with an elevated frequency of NAV behavior compared with products of 1-egg clutches and 2-egg clutches from which only 1 egg hatched.[9] This association implicates testosterone surges experienced during sibling conflicts as an organizing agent for adult abuse of unrelated nestlings,[8] in addition to its probable activational role in siblicide.[10] However, the ubiquity of NAV behavior among both siblicidal and nonsiblicidal individuals indicates that additional causes exist. We hypothesized that exposure to NAVs as a nestling may program a predisposition toward NAV behavior as an adult, in alignment with the cycle of violence hypothesis.

We collected daily breeding data, including band numbers of family members and siblicide history, and conducted systematic observations of NAVs in a subsection of a breeding colony on Isla Española, Galápagos Islands (1°23.4′S, 89°37.2′W), during three breeding seasons (2000–2001, 2001–2002, and 2002–2003; see Online Supporting Materials). During these observations, one or two observers walked back and forth along the edge of the "Study Area," scanning for NAVs with nestlings ("NAV events"). If a parent is present, it chases NAVs from the vicinity of the nest.[4] Thus, NAVs search for unguarded nestlings between roughly 30 and 80 days of age,[4] and this focused search behavior, their unique leg band numbers, their characteristic behavior when visiting a nestling, and the nestlings' reaction to them all distinguished NAVs from biological parents. The topography of the Study Area is flat and open, with clear lines of sight, so NAV events were detected as they began or shortly after. Our observations were facilitated by the fact that Nazca Boobies at this site are indifferent to close human presence. We made these observations daily from roughly 1300 to 1700 hours, when most NAV events occur,[4] during January–March, when most nestlings pass through an age-related window of vulnerability to NAVs.[4] Because NAV events were rare outside each season's period of observation, each nestling's history as a target of NAV behavior is essentially comprehensive.

During 2004–2005, we used the same methods to collect the same data from 24 of these birds as nonbreeding adults, documenting any NAV behavior as a perpetrator; the observers were blind to the history of these 24 birds and knew only that each one's history had been documented. Early in the 2004–2005 breeding season, we placed a conspicuous blue numbered leg band on each of the 24 focal birds to make them easily recognizable. Frequencies of aggressive, affiliative, and sexual behaviors were correlated strongly in these 24 birds as adults in 2004–2005 ($r_{agg-aff} = 0.783$, $P < 10^{-5}$; $r_{agg-sex} = 0.794$, $P < 10^{-5}$; $r_{aff-sex} = 0.883$, $P < 10^{-5}$), which suggests that NAV behavior is a unified syndrome rather than separate phenomena rooted in different causes. As predicted by the cycle of violence hypothesis, the number of NAV events that a nestling experienced showed strong positive relationships with the frequency of that individual's NAV behavior as an adult in 2004–2005, considering the total number of events experienced and also the frequencies of the three behavior types individually (Table 1 and Fig. 1), after controlling siblicidal experience. Because NAVs visit only nonfamilial young, these correlations imply that intergenerational transmission of the behavior is at least partially nongenetic.

Table 1. The relationship of frequency of nonparental adult visitor (NAV) behavior as an adult to three potential predictors, as determined by a generalized linear mixed-effects model for overdispersed Poisson regression. Each analysis included one or two predictors measured when the bird was a nestling (NAV events experienced by the focal bird and/or whether the focal bird was siblicidal), a random effect that accounts for how frequently the bird was present in the colony as an adult during the observation period, and an observation-level random effect that corrects overdispersion in the Poisson response variable. Significance (indicated by bold type) was determined using the false discovery correction for multiple comparisons.[26,27] To implement that correction, analyses are ranked by P value, and d_i equals the α_{crit} multiplied by the quantity (P value rank/n), with n equal to the number of P values estimated (in this case, 9). The largest P value less than the corresponding d_i value is considered significant ($\alpha_{crit} = 0.05$), as are all smaller P values.[26,27]

Predictor(s)	Coefficient (SE)	P	P-value rank	d_i
Affiliative events experienced	0.166 (0.0328)	**0.0000004**	1	0.006
Total NAV events experienced	0.076 (0.0181)	**0.00003**	2	0.011
Total NAV events experienced + siblicide	0.075 (0.0185)	**0.00005**	3	0.017
Affiliative events experienced + siblicide	0.164 (0.0387)	**0.00002**	4	0.022
Sexual events experienced	0.232 (0.0838)	**0.006**	5	0.028
Aggressive events experienced	0.112 (0.0482)	**0.021**	6	0.033
Sexual events experienced + siblicide	0.209 (0.0857)	**0.015**	7	0.039
Aggressive events experienced + siblicide	0.108 (0.0500)	**0.03**	8	0.044
Siblicide	0.477 (0.4048)	**0.24**	9	0.05

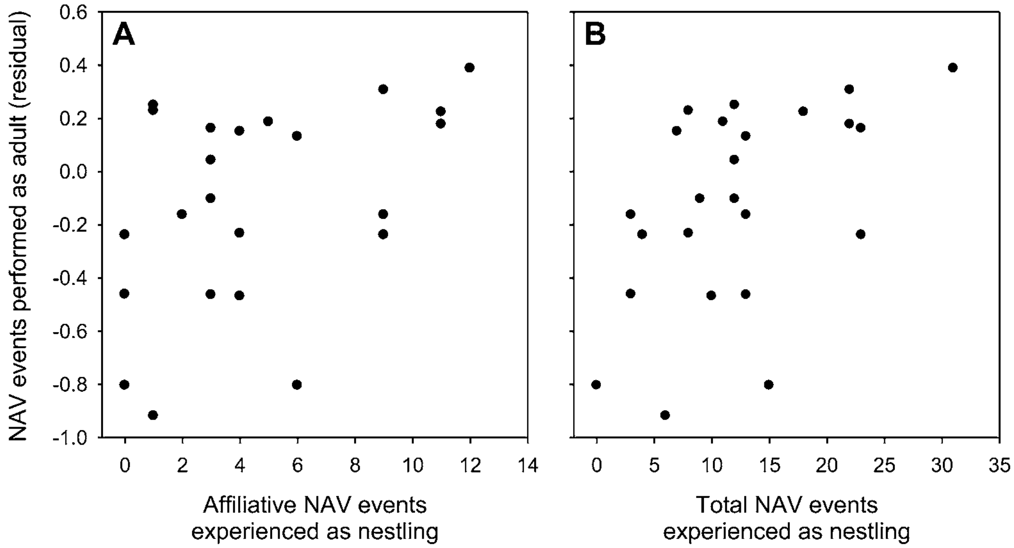

Fig. 1. Model residuals of (A) total nonparental adult visitor (NAV) events performed by adult Nazca Boobies on Isla Española, Galápagos Islands, in 2004–2005 that experienced a given number of affiliative NAV events as a nestling, and (B) total NAV events as a nestling. Model included two random effects: individual and number of nights present in the colony.

The high predictive ability of affiliative experience may be surprising, because aggressive and sexual behaviors may seem more invasive to the nestling. However, affiliative behavior is a good predictor of aggressive and sexual behavior, so nestlings can reliably assume that affiliative behavior presages more invasive maltreatment. Indeed, nestlings adopt the submissive "pelican posture" during all three types of interaction, which imposes thermoregulatory stress during the hottest part of the day by making evaporative cooling by gular fluttering impossible.[4]

The high repeatability of NAV behavior within adult individuals reveals it as a persistent characteristic of individual personality. For the two seasons with adequate samples (2002–2003 and 2004–2005), repeatability[11] (r) of the total number of NAV events recorded was 0.31 ($n = 176$, $P = 0.000002$). Separated into the three behavior types, repeatabilities were similarly high (affiliative: $r = 0.35$, $P = 0.00002$; aggressive: $r = 0.30$, $P = 0.00005$; sexual: $r = 0.21$, $P = 0.005$). The apparent conditioning of adult behavior by nestling experience (as a target of NAVs and as a participant in siblicide[8]) is, thus, likely to be lifelong, and may affect other aspects of personality.

The 24 nestlings experienced 0–31 NAV events as targets and perpetrated 1–56 events in 2004–2005, which indicates that adult behavior reflects the degree of their target experience in a continuous, rather than a qualitative, manner (Fig. 1). We found no significant associations between the frequency of NAV events experienced by nestlings and age or body condition at fledging, which suggests that social stress, rather than condition-related stress, drives the pattern of NAV behavior (Table 2). Our observations of these individuals do not suggest a role for any other variable in the association of nestling experience and adult behavior, except for parent attendance: nestlings that are guarded more by their parents experience fewer NAV events and perform fewer events later in life.[4] However, this correlational study cannot exclude a role for other variables.

This study and our earlier work[8] indicate that two different aspects of the nestling social experience condition this conspicuous element of adult behavior. The siblicide experience is ephemeral but intense, because it is a fight to the death,[10] and was revealed as a strong predictor of a NAV's behavior in 104 adults.[8] In the present study, a bird's history as a target of NAVs proved to be a much stronger predictor of its adult behavior than was its history of siblicide. (In fact, siblicide history did not reach statistical significance; we attribute that outcome to the much smaller sample size [$n = 24$] in the present study.) As we suggested with regard to the androgen surge that accompanies siblicidal behavior,[8] the intergenerational transmission of NAV behavior indicated by our present results may reflect an organizational effect of socially induced endocrine perturbations. We are focusing on the stress hormone corticosterone and the hypothalamic-pituitary-adrenal (HPA) axis as a probable candidate for physiological mediation of the cycle of violence in this species.[12]

The proximate-level causation of NAV behavior implicated by the separate cycle of violence and siblicide effects may provide a sufficient explanation for the phenomenon, without invoking any ultimate causation. A possible proximate-level scenario involves the prior evolution of adaptive siblicide under selection within an "insurance" framework.[9,13–15] Siblicide as a nestling appears to predispose Nazca Booby adults to NAV behavior,[8] so the behavior could come into existence by this means. Thereafter, both the siblicide effect and the cycle of violence can induce NAV behavior. In fact, intergenerational transmission may cause positive feedback: a single NAV can interact with many nestlings and, presumably, induce the NAV phenotype in all of them. An increase in the frequency of NAV behavior could occur over time under this scenario in the absence of selection for the behavior, and could even cross species boundaries: Nazca Booby NAVs also visit and maltreat Blue-footed Booby (*S. nebouxii*) nestlings[16] and could introduce a separate cycle of violence in that species. Members of at

Table 2. Results of mixed-effects regression predicting five indicators of growth, with nonparental adult visitor (NAV) events experienced as a nestling as a predictor and nestling sex and clutch size as random effects, for all 139 nestlings in the 4-year study. Degrees of freedom were 138 in all cases. "1% down age" is the age of the nestling when only 1% of its downy plumage remained, the rest having been replaced by pennaceous feathers. All measurements were taken on the day that the nestling reached the 1% down stage.

Predictor	Dependent variable	Coefficient (SE)	*t*	*P*
Total NAV events experienced	Body mass (g)	–1.50 (1.91)	0.79	0.43
	Culmen length (mm)	–0.025 (0.0240)	1.03	0.31
	Tarsus length (mm)	–0.010 (0.0190)	0.53	0.60
	Ulna length (mm)	–0.004 (0.0598)	0.07	0.94
	1% down age (*d*)	0.068 (0.0795)	0.86	0.39
Aggressive events experienced	Body mass	–0.91 (3.50)	0.26	0.80
	Culmen length	–0.017 (0.0440)	0.38	0.70
	Tarsus length	0.005 (0.0349)	0.14	0.89
	Ulna length	–0.050 (0.109)	0.46	0.65
	1% down age	0.126 (0.151)	0.84	0.40
Affiliative events experienced	Body mass	–5.15 (3.99)	1.29	0.20
	Culmen length	–0.080 (0.0501)	1.59	0.11
	Tarsus length	–0.005 (0.0349)	1.17	0.24
	Ulna length	0.015 (0.126)	0.12	0.90
	1% down age	0.135 (0.165)	0.82	0.41
Sexual events experienced	Body mass	–3.93 (14.9)	0.26	0.80
	Culmen length	–0.086 (0.187)	0.46	0.65
	Tarsus length	0.122 (0.146)	0.83	0.41
	Ulna length	0.459 (0.465)	0.99	0.32
	1% down age	0.091 (0.550)	0.17	0.87

least one Blue-footed Booby population exhibit NAV behavior at a lower frequency.[8] Of course, selection could act on NAV behavior, either favoring or disfavoring it in adults, and future work will explore this possibility. The behavior certainly has a negative effect on target nestlings, leading indirectly to fatal ectoparasitic blood-feeding by land birds in some years,[4] although growth is apparently not affected (Table 2).

Colonial birds may be a powerful model to study intergenerational transmission of maltreatment. The physical proximity among birds in a colony facilitates encounters among vulnerable youngsters and older, behaviorally dominant individuals. Young birds in colonies are typically easily detectable if older birds search for them, as is the case in Nazca Boobies.[4] Although aggressive targeting of nestlings of colonial birds has long been recognized[17] (including that induced by nestlings wandering close to unrelated adults[5]), sexual interest of adults toward young occurs but is relatively unappreciated. A number of bird species, including colonial taxa, exhibit this type of attraction to nestlings (Table 3). The third element of the behavior of Nazca Booby NAVs, affiliative attraction, may be common but overlooked because it can be mistaken for true parental care. We draw attention to all of these routes of attraction to nestlings, encouraging researchers to exploit these behaviors when they are detected to test the idea that experiences during development mold later social behavior. Of particular interest in the context of the cycle of violence would be the possibility of nongenetic intergenerational transmission of behavior, as is indicated by our results in Nazca Boobies.

Table 3. Sexual interactions that include copulation and courtship between adults and young in birds.

Species	Sex(es) involved	Attempted copulation partner	Frequency
Stitchbird (*Notiomystis cincta*)[20]	Males	Conspecific juvenile	3 individuals during 160 observation-hours
Yellow-rumped Cacique (*Cacicus cela*)[21]	Males	Conspecific nestling and juvenile	2% of adolescents with nestlings, 18% of adolescents with fledgling juveniles
Calliope Hummingbird (*Stellula calliope*)[22]	Males	Conspecific juvenile	1 individual
Anna's Hummingbird (*Calypte anna*)[23]	Males	Conspecific juvenile	1 individual
Black-billed Gull (*Larus bulleri*), Slender-billed Gull (*L. genei*), Red-billed Gull (*L. scopulinus*), and Black-headed Gull (*Chroicocephalus ridibundus*)[18]	Males	Conspecific nestling	Black-billed: 90 incidents in 6 days in a colony of 2,500. Other gulls: isolated incidents
Ring-billed Gull (*L. delawarensis*)[19]	Males and females	Conspecific nestling	"Appears to be low"
American White Pelican (*Pelecanus erythrorhynchos*)[24,25]	Males	Conspecific nestling (crèching)	At least 3 individuals in 41.5 h
Nazca Booby (*Sula granti*)[4]	Males and females	Conspecific and congeneric nestling	~80% of nonbreeders in a given year; ~100% of individuals over the lifetime

Acknowledgments

We thank the Galápagos National Park Service for permission to work in the Park and the Charles Darwin Research Station and TAME Airline for logistical support. The manuscript was much improved by the comments of K. Ashbrook, S. Forbes, and D. Mock. This material is based on work supported by the National Science Foundation under grants DEB 98-06606, DEB 0235818, and DEB 08-42199 to D.J.A. Please see the Supplementary Online Material for details about field and analytical methods (dx.doi.org/10.1525/auk.2011.11008).

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Associate Editor: M. T. Murphy