

### Interisland Variation in Blood Drinking by Galápagos Mockingbirds

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Few species of birds are known to feed on the blood of living animals, and the occurrence of this behavior in populations of the Sharp-beaked Ground-Finch (*Geospiza difficilis*) on Wolf and Darwin islands, Galápagos, has become notorious (Bowman and Billeb 1965, Köster and Köster 1983, Schlüter and Grant 1984). It is less widely recognized, however, that Galápagos mockingbirds (*Nesomimus* spp.) on some islands also drink blood from living hosts. Occasional blood drinking by mockingbirds on two islands was mentioned previously, but without details on the frequency or distribution of the trait (Bowman and Carter 1971, Christian 1980).

We observed blood drinking during studies of mockingbird cooperative breeding (Curry) and booby breeding biology (Anderson) between 1981 and 1985. Four endemic, allopatric mockingbird species inhabit the archipelago (Swarth 1931). We studied *N. macdonaldi* on Española; *N. trifasciatus*, the Floreana (Charles Island) Mockingbird, on Champion and Gardner-by-Floreana; *N. melanotis*, the San Cristóbal (Chatham Island) Mockingbird, on San Cristóbal; and *N. parvulus*, the Galápagos Mockingbird, on Darwin, Fernandina, Genovesa, Isabela, Santa Cruz, Santa Fe, Santiago, and Wolf. We studied color-banded birds on Genovesa (1981–1985), Champion (1981–1985), Española (1984–1985), and San Cristóbal (1984). On the other islands we observed unmarked birds during brief visits.

Mockingbirds (*N. macdonaldi*) on Española foraged in all habitats, eating fruit and both terrestrial and marine arthropods; the diet of mockingbirds on other islands is similar (Grant and Grant 1979, Curry unpubl. data). We observed Española mockingbirds drinking blood from living sea lions (*Zalophus californianus*), marine iguanas (*Amblyrhynchus subcristatus*), and nestling Masked Boobies (*Sula dactylatra*) in two locations near Punta Cevallos. Mockingbirds also twice attempted to drink blood from superficial wounds on the legs of field investigators.

On 27 December 1983 a wounded bull sea lion pulled out on an Española beach after receiving severe lacerations in its genital area during a fight with another male. Between 1400 and dusk at 1800 six banded mockingbirds drank blood directly from the sea lion's wounds while it lay on the beach. The bull left during the night, and the birds pecked at blood on the sand the next day. Mockingbirds also frequently obtained blood from sea lion placentas in one coastal area where

many sea lions gave birth. Up to four birds at a time fed from each placenta, eating tissues and drinking from pools of blood on the rocks.

We saw Española mockingbirds drink blood from living marine iguanas on four different occasions, all in 1984, in sections of rocky coast where iguanas were abundant. In each case the bird fed from a small hole in the iguana's tail until the victim moved into a protected position. *Nesomimus macdonaldi* may create these wounds incidentally while tearing off and eating ticks or skin from marine iguanas, as sometimes occurs when *N. parvulus* pecks ticks from land iguanas on Santa Fe (Christian 1980). On Española 25% of 100 iguanas examined had wounds like those from which we saw mockingbirds drink blood. In contrast, we found no such wounds on 100 iguanas at Isla Lobos and Cerro Brujo, San Cristóbal, where we did not see mockingbirds glean ticks or drink blood. We also saw several *N. macdonaldi* drink blood from the ground



Fig. 1. Mockingbird (*Nesomimus macdonaldi*) drinking blood from a conspicuous wound in the neck of a living Masked Booby (*Sula dactylatra*) nestling on Isla Española, Galápagos, while standing on the victim's head.

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TABLE 1. Blood drinking and associated behavior among Galápagos mockingbird (*Nesomimus* spp.) populations. Blood drinking includes only blood taken from living hosts; iguana pecking includes mockingbirds gleaning ticks or skin; carrion feeding includes only vertebrate sources. Host organisms are abbreviated as follows: marine iguanas (MI), land iguanas (LI), lava lizards or geckos (LG), seabirds (SB), sea lions (SL), tortoises (T), and goats (G). Behavior not observed on well-studied islands is indicated by a dash. Mockingbird behavior remains poorly known on islands indicated by a question mark. Sources of observations are denoted by footnotes.

Species	Island	Blood drinking	Iguana pecking	Carrion feeding
<i>N. macdonaldi</i>	Españaola <sup>a,b,c,d,e</sup>	SL, SB, MI	MI, LG	LG, MI, SB, G
<i>N. melanotis</i>	San Cristóbal <sup>a,f,g</sup>	—	MI	—
<i>N. trifasciatus</i>	Champion <sup>a</sup>	—	—	LG, SL, SB
<i>N. parvulus</i>	Gardner-by-Floreana <sup>a,h</sup>	?	?	SB
	Baltra <sup>i</sup>	?	?	LI
	Darwin <sup>a</sup>	—	?	?
	Fernandina <sup>a,b,j</sup>	—	MI, LI	LI
	Genovesa <sup>a</sup>	—	—	SB
	Isabela <sup>a,e</sup>	?	?	LG
	Marchena <sup>d,k</sup>	—	MI	LG
	Seymour	?	?	?
	Pinta <sup>k</sup>	—	?	LG
	Rábida	?	?	?
	Santa Cruz <sup>a,b</sup>	—	—	LG
	Santa Fe <sup>a,b,j,l</sup>	MI, LI	MI, LI	MI, G, SL
	Santiago <sup>a,m</sup>	?	?	T
	Wolf <sup>a</sup>	—	?	?

<sup>a</sup> This study.

<sup>b</sup> Bowman and Carter (1971).

<sup>c</sup> Amadon (1966).

<sup>d</sup> Carpenter (1966).

<sup>e</sup> Gifford (1919).

<sup>f</sup> Venables (1940).

<sup>g</sup> Bowman (pers. comm.).

<sup>h</sup> Harris (1968).

<sup>i</sup> Beebe (1924); population now extinct.

<sup>j</sup> Christian (1980).

<sup>k</sup> Schlüter (pers. comm.).

<sup>l</sup> A. Laurie (pers. comm.).

<sup>m</sup> Darwin (1841).

after a Galápagos Hawk (*Buteo galapagoensis*) killed and removed an iguana (see Bowman and Carter 1971).

Españaola mockingbirds obtained blood more frequently from seabirds than from sea lions or iguanas. We observed mockingbirds drinking blood from 9 different Masked Booby nestlings (25–50 days old) in 1984 and from another 22 in 1985, in an area at Punta Cevallos of roughly 300 booby nests. Españaola mockingbirds also attack Blue-footed Boobies (*S. nebulouxii*; Nelson 1968) and Waved Albatross (*Diomedea irrorata*) chicks (S. Harcourt pers. comm.), but we saw no mockingbirds drink blood from these species. Most, if not all, of the 31 victims had been assaulted by nonparental adult Masked Boobies, resulting in abrasions and lacerations on the chicks' necks, heads, rumps, and wings. We do not know why these assaults (Nelson 1978: 385) occurred, but the wounds clearly attracted mockingbirds. [Finches (*G. difficilis*) on Wolf feed from booby nestlings wounded in the same way (Köster and Köster 1983).] When first attacked, booby chicks deterred mockingbirds temporarily by jabbing

with their bills. Parental boobies also defended their chicks and occasionally may have killed blood drinkers: we found the bodies of four mockingbirds, including a banded individual that previously drank blood from a booby nestling, next to nests containing booby chicks. During long intervals when booby parents left the nest to forage, blood drinking by mockingbirds was interrupted only when nonparental boobies resumed their assaults on the chicks. Attacking mockingbirds gathered around each victim and attempted to perch on its back or head to eat tissue and drink blood (Fig. 1). In a few cases we saw only one mockingbird drink blood from a chick, but usually several did so (mean minimum number of feeders =  $4.3 \pm 5.1$  SD,  $n = 28$ ). As each victim's condition deteriorated and it became increasingly unresponsive, more blood drinkers joined in. In one case at least 35 mockingbirds fed from a single booby nestling just before it died. Most victims died within 24 h of the onset of blood drinking, usually after their vertebral columns and spinal cords were exposed.

At least 38% of the 55 mockingbirds resident at Punta Cevallos drank booby blood one or more times, and some individuals alternated between two victims in a single day. Birds from other parts of the island where seabirds did not nest also drank blood from boobies at Punta Cevallos; three of the banded *N. macdonaldi* we saw drinking blood held territories 2 km away.

Our data are insufficient to determine what proportion of the diet of mockingbirds on Española consists of blood. The fact that mockingbirds avidly exploit all available sources of blood suggests that blood is a preferred food. Blood drinking may occur predominantly during dry seasons when other foods are scarce. The blood drinking we observed took place during dry periods in both 1984 and 1985. Blood drinking was less frequent under wetter conditions in 1986 (Anderson pers. obs.).

Information available about other islands indicates that there is considerable interisland variability in blood drinking and related behavior among Galápagos mockingbird populations (Table 1). In Table 1 we have listed all known records of blood drinking from living hosts; we also include observations of mockingbirds removing ticks or skin from iguanas ("iguana pecking") or feeding on carrion, because most of the few other known blood-eating bird species feed on ectoparasites or carrion, or both (Bowman and Billeb 1965). After Española, blood drinking occurs most frequently on Santa Fe, where mockingbirds (*N. parvulus*) occasionally drink blood from land iguanas (*Conolophus pallidus*; Christian 1980) and from marine iguanas wounded by hawks or sharks (A. Laurie pers. comm.). Blood drinking is not known to occur in any other Galápagos mockingbird population. *Nesomimus parvulus* on Genovesa has not been seen drinking blood from any living hosts, though mockingbirds have been studied intensively there since 1978 using field methods identical to those we used on Española (Grant and Grant 1979, Kinnaird and Grant 1982, Curry 1985, pers. obs.). Anderson saw finches (*G. difficilis*), but no mockingbirds, drink blood from seabirds on Wolf and Darwin in 1981. We found no evidence of blood drinking in *N. parvulus* on Santiago, Isabela, Fernandina, or Santa Cruz. Mockingbirds (*N. trifasciatus*) on Champion feed on carrion, and on Gardner-by-Floreana they occasionally kill seabird chicks (Harris 1968), but we did not observe iguana pecking or blood drinking on either islet. No blood drinking or carrion feeding has been reported in *N. melanotis*. The birds we studied at three locations on San Cristóbal (Playa Baquerizo, Cerro Brujo, El Junco) foraged arboreally and did not attempt to feed from iguanas or seabirds, but Bowman (pers. comm.) saw *N. melanotis* pecking ticks from marine iguanas at another location (Punta Pitt).

The occurrence of blood drinking and associated behavior by mockingbirds on some islands, combined with their apparent absence on others, raises ques-

tions about the origin of these unusual traits. It is not surprising that some Galápagos mockingbirds should drink blood because all forage opportunistically (Beebe 1924, Amadon 1966, Bowman and Carter 1971, Grant and Grant 1979, Curry 1986), in common with the few other species of blood-drinking birds (Bowman and Billeb 1965). This factor does not explain why blood drinking is restricted to just a few populations.

Unlike egg eating by Galápagos mockingbirds (Bowman and Carter 1971), there is no simple correspondence between blood drinking and ecological setting, mockingbird morphology, or the distribution of hosts among the islands. Española, Santa Fe, and Genovesa are small, low, and arid islands where mockingbirds are among the longest-billed forms (Swarth 1931). Blood drinking occurs on Española and Santa Fe but not on Genovesa. Potential sources, including sea lions (Eibl-Eibesfeldt 1984a), iguanas (Eibl-Eibesfeldt 1984b), and nesting seabirds (Harris 1973), occur virtually throughout the archipelago. Additional factors must be invoked to explain why blood drinking is not common to all arid-island populations.

Variation in social behavior among Galápagos mockingbird populations may account partially for the distribution of blood drinking. If specialized feeding techniques, including blood drinking, are learned (Bowman and Billeb 1965, Christian 1980), such traits may become established in socially complex populations in which opportunities for learning occur frequently, as suggested for tick pecking in *Aphelocoma coerulescens* (Baber and Morris 1980, Isenhart and DeSante 1985). Galápagos mockingbirds have complex social organizations that include group territoriality and cooperative breeding (Hatch 1966, Grant and Grant 1979, Kinnaird and Grant 1982, Curry 1987). With some variation these factors correlate with blood drinking. Mockingbirds in coastal areas of Española, where blood drinking is most frequent, live in large groups (up to 17 birds) at high density (9–16 birds/ha); on Santa Cristóbal, where blood drinking is not known to occur, mockingbirds live in much smaller groups (2–3 birds) at lower density (less than 1 bird/ha) (Curry 1987). However, mockingbirds live in moderately large groups (averaging 3–4 birds) at high density (4 birds/ha) on Champion and Genovesa (Curry 1987) but do not drink blood, so social complexity alone does not fully account for the distribution of blood drinking.

We suggest that interisland variation in blood drinking may result from differences in the frequency of opportunities to sample blood, which could arise in at least two ways. First, blood should be more often available to mockingbirds on islands where Galápagos Hawks kill or wound large prey such as iguanas or seabirds than on islands without hawks. A role for hawks in mockingbird blood drinking is supported by the observation that hawks are resident on Española and Santa Fe, where mockingbirds drink blood,

but hawks are absent from Genovesa, Champion, Darwin, Rábida, San Cristóbal, Santa Cruz, Seymour, and Wolf (Harris 1973), islands where mockingbirds are not known to drink blood. Blood drinking by mockingbirds could be expected on other islands with resident Galápagos Hawks (Isabela, Fernandina, Marchena, Pinta, and Santiago), but foraging patterns in these mockingbird populations are not sufficiently well known to test this prediction. Mockingbirds also might be exposed to blood from smaller animals killed by Short-eared Owls (*Asio flammeus*) or Common Barn Owls (*Tyto alba*). The distribution of neither of these predators, however, coincides with the pattern of blood drinking among mockingbird populations. *Asio* inhabits all principal islands, including those where mockingbirds do and do not drink blood, and *Tyto* is absent from Española, where blood drinking by mockingbirds is most conspicuous.

Mockingbirds could be differentially exposed to blood through iguana pecking. Mockingbirds that glean ectoparasites from iguanas would have frequent opportunities to sample blood. Generalized blood drinking may have derived from a protocooperative association between mockingbirds and iguanas (Christian 1980, Isenhart and DeSante 1985; see also Bowman and Billeb 1965). Consistent with this hypothesis, mockingbirds most frequently drink blood on islands where they also peck at iguanas (Table 1), although mockingbirds have been seen pecking at iguanas on two other islands (Fernandina and San Cristóbal) where no blood feeding has been reported. Furthermore, the hypothesis fails to explain why the tendency to peck at iguanas varies among mockingbird populations.

Unless additional factors can account for variation in iguana pecking by mockingbirds, the hypothesis that hawks indirectly influence mockingbird blood drinking is better supported by the information available. It remains possible, however, that blood drinking arose simply by chance in just two populations. Regardless of which explanation for the distribution of blood drinking is correct, *N. macdonaldi* on Española has evolved an exceptional tendency to exploit blood from any available source.

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### Further Evidence of Long-term Pair Bonds in Ducks of the Genus *Bucephala*

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In holarctic ducks, pair formation occurs during the winter or the spring migration, or both, and pair bonds are seasonal, usually lasting until the onset of incubation by the female (McKinney 1986). Because males desert their mates during incubation and leave the breeding grounds for molting, it has been thought that new pair bonds are formed every year and that repairing with the same mate does not occur (Rowley 1983, McKinney 1986). In dabbling ducks, marking males on the breeding grounds has confirmed that long-term pair bonds (>1 yr) do not occur (Poston 1974, Blohm 1978), although exceptions exist (e.g. Dwyer et al. 1973). In seaducks, however, there is evidence that pairing with the same individual for more than one breeding season may be a common occurrence. Savard (1985a) recently reported that in Barrow's Goldeneye (*Bucephala islandica*) the return rates of adult males and females to the breeding grounds were similar (66% vs. 76%), and that several pairs reunited in subsequent years. I now present evidence that male Buffleheads (*B. albeola*) are also philopatric to their breeding area and that pair bonds can reform in subsequent years.

The study was conducted in the Cariboo Parkland of British Columbia. In 1983 I captured 3 male Buffleheads using a mirror trap (Savard 1985b), whereas 66 females were trapped on the nest between 1982 and 1985. All birds were marked individually with color-coded nasal saddles and a set of color bands. In

all cases the mates of marked males were marked. Retention of saddles was poor after 2 yr, but the leg bands enabled me to identify individuals up to at least 4 yr.

Pair 1 consisted of the same individuals in 1983 and 1984. This pair was not seen on the study area in 1985, but female 1 returned in 1986 with a new mate. From 1982 to 1984, and again in 1986, female 1 nested successfully in the same tree cavity, and her mate always defended the same territory, located on the pond closest to her nest. The reasons for her absence in 1985 are unknown as both the cavity and territory were unoccupied.

Pair 2 involved the same male and female for at least three consecutive seasons. Female 2 failed to hatch a clutch in all years and changed nest sites every year. The pair changed ponds from 1983 to 1984 but not in 1985. In 1986 male 2 returned unpaired for a fourth year to the same pond. His former mate did not return to the study area. For much of the nesting season he remained on the same pond, where he joined transient groups of nonbreeders and performed courtship displays to unpaired females.

Pair 3 nested successfully in 1983 but was not seen subsequently on the study area. Male 3, however, was known to be alive in the following year because he was resighted on the wintering area near San Diego, California, in December 1984 (T. Meyer pers. comm.).

Two of the three marked pairs, therefore, remained intact for 2 yr and one of them for a third year. Buffleheads are highly territorial during the breeding season (Gauthier 1987), and philopatry of females to the territory is high (Erskine 1961, Gauthier in prep.). My results show that philopatry may also be strong

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