

# Grooming Time Predicts Survival: American Kestrels, *Falco sparverius*, on a Subtropical Island

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**ABSTRACT:** Animals have evolved a variety of adaptations to care for their body surfaces, such as grooming behavior, which keeps the integument clean, parasite-free, and properly arranged. Despite extensive research on the grooming of mammals, birds, and arthropods, the survival value of grooming has never been directly measured in natural populations. We monitored grooming and survival in a population of marked American kestrels (*Falco sparverius*) on San Salvador Island, Bahamas. We found a strong association between time spent grooming and survival over a 2-year period. The quadratic relationship we show is consistent with stabilizing natural selection on grooming time. To our knowledge, this is the first evidence for a correlation between grooming time and survival in a natural population. Grooming time may predict the survival of many animal taxa, but additional studies are needed to determine the shape and strength of the relationship among birds, mammals, and arthropods.

**Keywords:** preening, scratching, antiparasite behavior, bird, lice.

The part played by natural selection in evolution cannot be assessed without proper study of survival value. (Tinbergen 1963)

## Introduction

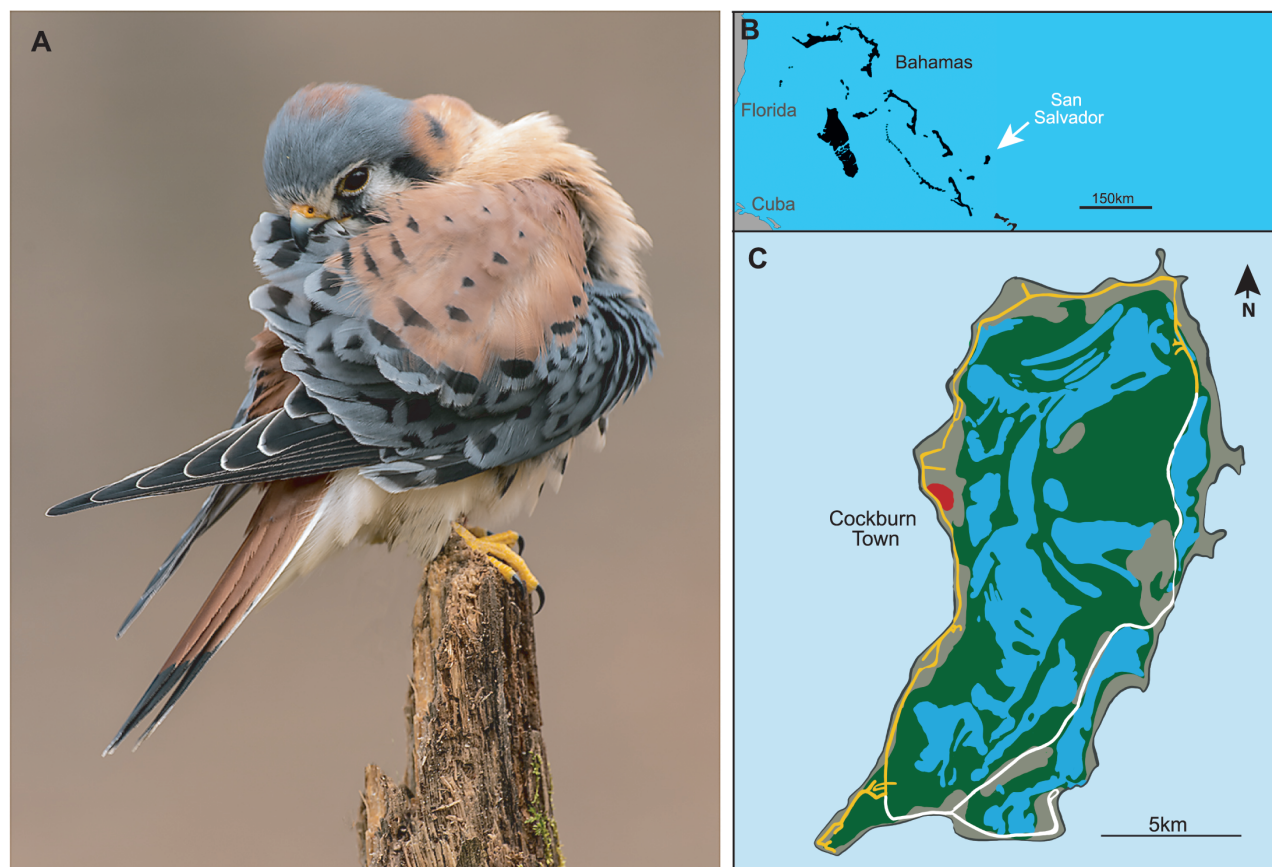
Animals have evolved morphological, physiological, and behavioral adaptations to care for their body surfaces (Borchelt 1980; Amador and Hu 2015). These adaptations include behaviors such as grooming, dusting, bathing, and sunning (Spruijt et al. 1992; Clayton et al. 2010; Zhukovskaya et al. 2013). Hundreds of studies of grooming by mammals, birds, and arthropods have been published, yet most of these concern proximal questions, such as the neurobiological, endocrinological, and genetic bases of grooming

(Sachs 1988; Spruijt et al. 1992; Kalueff et al. 2010; Yanagawa et al. 2020; Zhang et al. 2021). Ultimate questions related to the adaptive function and evolution of grooming have received less attention. Understanding the ultimate basis of grooming requires documentation of variation among individuals in natural populations and determination of the fitness consequences of this variation (Tinbergen 1963; Bateson and Laland 2013; Nesse 2013). Here we document the variation and correlated fitness consequences of grooming in a wild bird population.

Avian grooming consists of preening with the bill (fig. 1A) and scratching with the feet (Clayton and Cotgreave 1994; Clayton et al. 2015). Preening cleans and arranges feathers, “zips” the barbules of flight feathers together, distributes preen oil and powder down, and combats ectoparasites (Simmons 1985). Scratching with the claws controls ectoparasites on the head and neck by “flushing” them to lower regions of the body, where they can be killed or removed by preening (Goodman et al. 2020). Scratching also helps spread preen oil over the head feathers (Simmons 1985). Most species of birds spend 5%–15% of their time preening, with an energetic cost that is 1.6–2.3 times that of basic metabolic rate (Clayton et al. 2015). The time and energy required for grooming, at the expense of other activities, such as foraging and breeding, means that grooming is likely to create trade-offs that may have fitness consequences.

We studied the grooming behavior of a natural population of American kestrels (fig. 1A) living on San Salvador Island, Bahamas (fig. 1B, 1C). One goal of our study was to quantify variation in grooming behavior in the population. Another goal was to estimate ectoparasite loads to test whether parasite load covaries with grooming time, survival, or both. Control of ectoparasites—particular chewing lice (Insecta: Phthiraptera)—is an important function of avian grooming (Clayton et al. 2010; Bush and Clayton 2018). The most important goal of our study was to explore

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**Figure 1:** A, American kestrel (*Falco sparverius*) preening wing coverts (photo by Andy Byerly). B, San Salvador Island is located along the eastern edge of the Bahama archipelago (24°N, 74°30'W). C, San Salvador Island (redrawn from Smith 1993). Blue indicates inland lakes and tidal creeks; green indicates blacklands (coppice); gray indicates kestrel habitat; red indicates Cockburn Town, the island's civic center; yellow indicates the study transect (roads with telephone poles/wires, 40 km); and white indicates roads that were not part of the study transect (without poles/wires, 30 km).

the survival of birds in relation to the amount of time they spent grooming.

## Methods

### Study Site

Estimating the survival of wild birds is challenging because of the difficulty in distinguishing mortality from dispersal (Newton et al. 2016). One way to simplify the task is to study a population of nonmigratory birds on a small, isolated island like San Salvador (fig. 1B, 1C). This subtropical island is surrounded by oceanic water more than 1,000 m deep. The nearest islands of any size are Cat Island, 72 km to the west-northwest, and Rum Cay, 37 km to the south-west. San Salvador is small (~20 km long, ~11 km wide) with an area of ~157 km<sup>2</sup>. About 30% of its interior consists of tidal creeks and hypersaline lakes (fig. 1C; Kass et al. 2018). Much of the rest of the island is covered by lowland scrub habitat unsuitable for kestrels, such as black-

lands (coppice), which have dense thickets that cannot be penetrated without a machete (Smith 1993).

Kestrels on San Salvador are members of a nonmigratory subspecies of the American kestrel (*Falco sparverius sparveroides*) that is endemic to the Bahamas, Cuba, and the Isle of Pines (del Hoyo et al. 1994). The North American subspecies *Falco sparverius sparverius*, which is migratory and winters on some northern Bahama islands (Smallwood and Bird 2020), does not occur on southern islands, such as San Salvador (Paulson 1966; Miller 1978; Hallet 2006; S. E. Bush and D. H. Clayton, personal observations). San Salvador kestrels are abundant and relatively tame, making them easy to capture, mark, and observe.

Most kestrel habitat on San Salvador is restricted to coastlines where blacklands habitat transitions to open beaches, as well as agricultural, residential, and other disturbed areas within a few hundred meters of the coast. A narrow asphalt road runs through most of this habitat. On the north and west sides of the island, the road is bordered

by short telephone poles supporting telephone/power lines that are heavily used by kestrels. This 40-km stretch of the road defined our study transect (fig. 1C). The 30-km stretch of road running along the south and east sides of the island is more exposed to extreme weather and has no active settlements, poles, or lines. We did not band kestrels on this part of the island.

#### *Bird Banding and Measurements*

Fieldwork was initiated in 2019, following the kestrel breeding season. From July 19 to August 3, we used Bal-Chatri traps to capture kestrels. Upon capture, each bird was fitted with a falconry hood to minimize stress (Madden and Mitchell 2018). The bird's legs were gently bound with a strip of Velcro to immobilize the talons. Each bird was weighed with a Pesola balance, and the (unflattened) left wing chord was measured. Other standard measurements of the bill and tarsus were taken for a related study. Body condition was determined using body mass and wing chord to calculate a scaled body mass index (Peig and Green 2009).

Seventy-two birds were each fitted with a numbered aluminum band and unique combination of three Darvic plastic bands of five possible colors: white, yellow, blue, green, and red. After being released at the capture site, some birds pulled at their bands for several hours or days following banding. Most birds soon ignored their bands.

#### *Survival*

Efforts to resight banded birds took place from November 11 to December 11, 2019, following the rainy season from August to October, and again at the end of the study from July 4 to July 19, 2021 (fig. S1). (We were unable to visit San Salvador in 2020 because of the COVID-19 pandemic.) We observed birds while we were walking or driving slowly (~25 km/h) along the 40-km study transect each day. Kestrels are easy to observe because they prefer to hunt from prominent perches (Hinnebusch et al. 2010). During these drives, two observers scanned for kestrels on opposite sides of the road. When a bird was located, the observers used spotting scopes to identify the color band combination of the bird. Most birds retained all three of their color bands, in addition to the aluminum band. By 2021, four birds had lost one color band each, but we were able to identify all four birds by process of elimination.

Although we did not band birds on the south and east sides of the island, we checked for dispersal of banded birds to these locations by routinely driving slowly along the south and east road. We typically saw 10 or more kestrels, and we examined the legs of these birds carefully with spotting scopes. Banded birds were never observed in

this area. There was thus no evidence that any of the banded kestrels from our study transect dispersed across the island, even over a 2-year period.

#### *Grooming*

Approximately 1 week after birds were banded, we began collecting data on the grooming behavior of each bird. We observed birds with binoculars and spotting scopes while recording their behavior using the Animal Behaviour Pro app for iPhone (Newton-Fisher 2021; van der Marel et al. 2021). Each bout of grooming was considered complete when a bird stopped for more than 3 s or switched to a different behavior (Clayton and Cotgreave 1994). We restricted analyses of grooming behavior to the 33 kestrels for which we collected at least 1 h of behavioral data. The mean ( $\pm$ SE) amount of grooming data, per bird, was  $97.7 \pm 4.0$  min, with a minimum of 62.3 min and a maximum of 174.2 min. We collected data from each bird on five different occasions, on average, with data from both morning and afternoon for 31 of the 33 (94%) birds and data from both summer (July to August) and autumn (November to December) for 29 of the 33 (88%) birds (fig. S2).

#### *Ectoparasites*

Parasite data were collected during November and December of 2019. We retrapped banded birds and used a two-step procedure to collect parasite data. First, each bird was held on its back in one hand while one of us (D. H. Clayton) searched for ectoparasites while deflecting feathers of the throat (gulum), breast, belly, and cloacal region (crissum) with forceps. Representative samples of ectoparasites were removed and placed in 95% ethyl alcohol. The goal of this step was to document the ectoparasite community on San Salvador kestrels. The kestrels were parasitized by two species of chewing lice: *Degeeriella carruthi* (Ischnocera) and *Colpocephalum subzerafae* (Amblycera; Price et al. 2003; voucher specimens deposited in the Price Institute of Parasite Research, University of Utah, PIPR020001 and PIPR020002, <https://scan-bugs.org>). No other ectoparasites (insects, mites, or ticks) were observed on any of the kestrels.

The second step involved quantification of the number of eggs of lice. Chewing lice are “permanent” parasites that complete their entire life cycle on the body of the host. Louse eggs are glued to the feathers with a glandular cement. Like other members of the genus *Colpocephalum* (Nelson and Murray 1971), *C. subzerafae* attaches its eggs between feather barbs on the ventral side of flight feathers of the wing (primaries 1–6 and, occasionally, secondaries 1–3). When the egg hatches, the top (operculum) pops off like a cap, leaving most of the empty egg shell attached to the feather. One of us (D. H. Clayton) used an  $\times 8$ –35 Labomed Luxeo

4Z stereomicroscope to count *C. subzerafae* eggs (hatched and unhatched) on the ventral sides of primary and secondary feathers, as well as the tail feathers (rectrices); no eggs were ever found on the tail. This method records the cumulative number of louse eggs deposited since the last molt. *Degeeriella carruthi* eggs were not counted because their site of deposition remains undiscovered (louse eggs are very small).

### Analyses

Survival and resighting probabilities were estimated in the program MARK (ver. 9.0; White and Burnham 1999). We selected the Cormack-Jolly-Seber framework to estimate time-constant survival ( $\phi(\cdot)$ ) and resighting ( $p(\cdot)$ ) probabilities using maximum likelihood estimation methods (Lebreton et al. 1992; Williams et al. 2002). The highest-ranking (best-fitting) model was determined to be the one with the lowest corrected Akaike information criterion (AICc) value (Burnham and Anderson 2002), and any model with AICc  $\geq 2$  was determined to have limited support from the data (Williams et al. 2002). Additional analyses were conducted in JMP (ver. 16; SAS Institute, Cary, NC, 1989–2021).

### Results

#### Survival

The estimated annual probability of survival ( $\pm$ SE) for kestrels in this population is  $0.62 \pm 0.05$ , and the estimated probability of resighting is  $1.00 \pm 0.00$  (model:  $\phi(\cdot)p(\cdot)$ ; bootstrap goodness of fit,  $P = .99$ ). Of the 72 banded birds, 57 were resighted in November and December 2019, and 29 were resighted again in July and August 2021. No birds were resighted in 2021 that had not been resighted in November and December 2019.

#### Grooming

We collected at least 1 h of behavioral data for each of 33 individually marked kestrels. Birds spent a mean ( $\pm$ SE)

of  $12.0\% \pm 1.4\%$  of their time grooming, divided between preening ( $91.7\% \pm 1.5\%$ ) and scratching ( $8.3\% \pm 1.5\%$ ). The time that individuals spent grooming was not consistent between seasons (Pearson  $r_{29} = -0.003$ ,  $P = .98$ ), and it was not consistent between morning and afternoon within each season (summer,  $r_{15} = -0.40$ ,  $P = .14$ ; autumn,  $r_{20} = 0.24$ ,  $P = .31$ ). Grooming was not correlated with body condition (linear regression,  $F_{1,32} = 0.15$ ,  $R^2 = 0.005$ ,  $P = .70$ ).

#### Ectoparasites

We obtained parasite data from 30 of the 33 kestrels in the study (three birds were not retrapped); 26 of the 30 birds (87%) had lice and/or their eggs. Five kestrels (17%) had one to three hatched *Colpocephalum subzerafae*, and 24 kestrels (80%) had *C. subzerafae* eggs. The number of eggs observed among the infested birds (one wing) varied from 1 to 384 (fig. S3A). Three kestrels (10%) had one or two hatched *Degeeriella carruthi*. Two of the kestrels with hatched *D. carruthi* were coinfecting with *C. subzerafae* eggs. *Colpocephalum subzerafae* egg abundance (log + 1 transformation) was independent of body condition (fig. S3B; linear regression,  $F_{1,29} = 0.57$ ,  $R^2 = 0.02$ ,  $P = .46$ ). Egg abundance was also independent of host grooming time (fig. S3C; linear regression,  $F_{1,29} = 1.36$ ,  $R^2 = 0.05$ ,  $P = .25$ ).

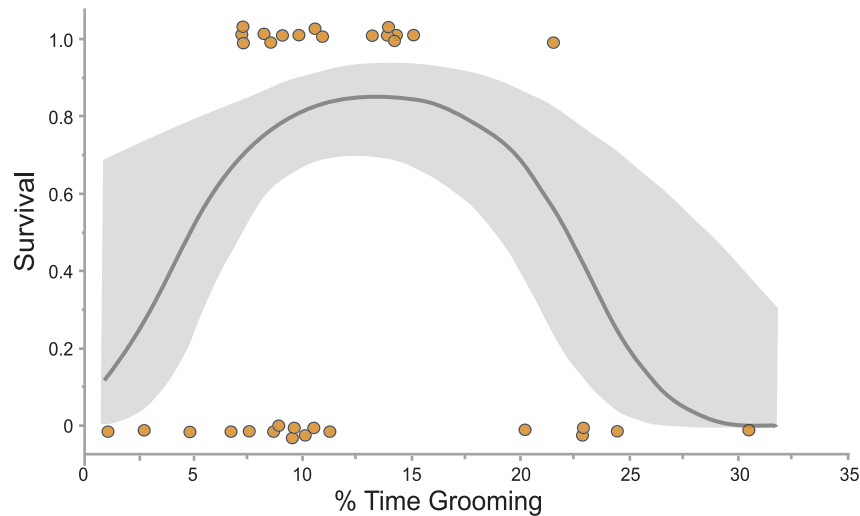
#### Correlates of Survival

We explored whether body condition, parasite abundance, and time spent grooming covaried with survival for the 33 kestrels in our restricted data set. In all, we built six models (table 1). Survival was best described by a model incorporating a quadratic function of grooming time (table 1), with kestrels that groomed an intermediate amount of time having the highest probability of annual survival (fig. 2). Models using a linear function of grooming, or including other covariates, had AICc scores that were  $\geq 7.78$  units higher than the best model (table 1), indicating that kestrel

**Table 1:** Model selection for covariates of kestrel survival

| Model                                              | AICc         | $\Delta$ AICc | AICc weight | Model likelihood | Parameters | Deviance     |
|----------------------------------------------------|--------------|---------------|-------------|------------------|------------|--------------|
| $\phi(\text{groom} \times \text{groom}^2)p(\cdot)$ | <b>54.57</b> | <b>.00</b>    | <b>.93</b>  | <b>1.00</b>      | <b>3</b>   | <b>48.17</b> |
| $\phi(\text{parasite})p(\cdot)$                    | 62.33        | 7.78          | .02         | .02              | 2          | 58.13        |
| $\phi(\text{groom})p(\cdot)$                       | 62.68        | 8.11          | .02         | .02              | 2          | 58.49        |
| $\phi(\text{SBMI})p(\cdot)$                        | 63.05        | 8.48          | .01         | .01              | 2          | 58.85        |
| $\phi(\cdot)p(\cdot)$                              | 63.38        | 8.81          | .01         | .01              | 2          | 59.18        |
| $\phi(\text{SBMI} \times \text{SBMI}^2)p(\cdot)$   | 64.79        | 10.22         | .01         | .01              | 3          | 58.39        |

Note: Models are listed in order of corrected Akaike information criterion (AICc) rank, with the most supported model (bold) listed first. All models tested are shown. Covariates include the percentage of time kestrels spent grooming (groom), body condition calculated as scaled body mass index (SBMI), and the abundance of louse eggs (parasite). Quadratic models were investigated for grooming behavior and body condition. Models assume a time-constant probability of survival ( $\phi(\cdot)$ ) and resighting ( $p(\cdot)$ ) and apply a logit link function. Bootstrap goodness of fit for model without covariates  $\phi(\cdot)p(\cdot)$ ,  $P = .97$ .



**Figure 2:** Grooming time predicts survival in a natural population. Points indicate kestrels that were resighted ( $=1$ ) or not ( $=0$ ) 2 years after they were banded (points jittered on  $y$ -axis for clarity). The gray line shows the estimated probability of survival (95% confidence interval shaded) derived from the most supported model (table 1) generated in MARK version 9.0.

survival was independent of body condition and parasite abundance.

### Discussion

We studied a wild population of kestrels to document variation in grooming behavior and whether this variation relates to the survival component of fitness. Using a Cormack-Jolly-Seber framework, we estimated the survival and resighting probabilities for 72 kestrels banded in July and August 2019 that were resurveyed after 4 months and again after 24 months. The estimated annual survival probability of kestrels in this population was 62% ( $\pm 5\%$ ), which is slightly lower than the annual survival rate of 74%–75% estimated for American kestrels in Florida (Hinnebusch et al. 2010). All birds resighted at the end of the study had also been resighted 4 months after initial capture and banding, yielding an extremely high resighting probability ( $p = 1.00 \pm 0.00$ ).

We collected at least 1 h of data on the grooming behavior of a subset ( $n = 33$ ) of the banded kestrels. Overall, birds spent a mean of 12.2% of their time grooming, most of which consisted of preening with the bill. Among individuals, grooming varied from 1.2% to 30.4% of the time. Individual birds were not consistent in grooming time between seasons or between morning and afternoon within a season. In the future, grooming data collected over shorter time intervals may facilitate a more informative test of individual consistency, which is an important goal.

The relationship between grooming time and survival was best modeled by a quadratic function (fig. 2). The likelihood of survival was highest among birds that groomed

intermediate amounts of time. With the exception of a single bird that groomed 21% of the time, all surviving birds groomed from 7% to 15% of the time. No bird that groomed  $<7\%$  of the time survived, and only one bird that groomed  $>16\%$  of the time survived.

Survival was independent of parasite abundance, which, in turn, was independent of host body condition and grooming time. Experimental work shows that grooming is an effective defense against ectoparasites (Clayton et al. 2010, 2015) and that increases in feather lice trigger increases in grooming (Villa et al. 2016). In the absence of experimental manipulation, however, louse abundance and grooming may show negative frequency dependence. An increase in lice may trigger an increase in grooming, causing a decrease in lice, which then causes a decrease in grooming. Unless the dynamics of the lice and grooming are tightly linked, a pattern like the one in figure S3C can result.

In this study, sources of mortality for birds with low versus high grooming rates could have been different. Low groomers may have suffered from poor plumage quality, given the central importance of grooming for anointing plumage with preen oil. The hypothesized functions of preen oil are many, including waterproofing feathers, combatting feather-degrading bacteria, facilitating odor-based communication between birds, and even reducing aerodynamic drag in flight (Moreno-Rueda 2017). Low grooming rates may also have been symptomatic of other problems. Avian malaria is known to reduce preening rates in birds that eventually succumb to the malaria itself (Yorinks and Atkinson 2000). Nothing is known about the prevalence of avian malaria on San Salvador; however, malaria is generally common among birds in the Caribbean (Fallon et al. 2005).

In contrast, the cause of mortality for birds with high grooming rates may have been related to stress. Elevated grooming rates are a common symptom of stress in birds, indicated by higher baseline corticosterone levels (Langlois 2021). Endocrinological assays, in conjunction with monitoring of grooming rates and survival, may allow this hypothesis to be tested.

Our results parallel those of Lewis et al. (2007), who showed a positive correlation between allopreening, a form of social grooming, and reproductive success in common guillemots (*Uria aalge*), which are colonial seabirds. Allopreening between mates was correlated with long-term reproductive success, while allopreening between densely packed neighbors was correlated with short-term reproductive success. The authors of the guillemot study hypothesized that allopreening modulated social stress in the nesting birds they studied. The kestrels in our study did not allopreen but preened only themselves.

Despite the fact that birds (Aves) are one of the best-observed and best-understood classes of organisms on Earth, their grooming behavior has been relatively ignored (Clayton et al. 2010; Bush and Clayton 2018). To our knowledge, this is the first study to show a relationship between grooming and survival in birds. Remarkably, the survival of kestrels over a 2-year period could be predicted with considerable accuracy from a mean of only about 100 min of behavioral data collected in the first 6 months of the study.

More broadly, we believe that this is the first study to show a correlation between grooming and survival in any animal population. Our results are consistent with stabilizing selection on grooming time. Because our data are observational, we cannot rule out the possibility that grooming time and survival are jointly influenced by one or more other causal agents. Our results provide strong incentive for additional work, including experimental manipulation of factors that covary with grooming and survival, such as the quantity and quality of preen oil produced by individual birds. Birds, mammals, and arthropods all groom on a regular basis. We suggest that grooming time is an important component of the evolutionary fitness of a variety of animal taxa.

### Acknowledgments

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### Statement of Authorship

S.E.B. and D.H.C. conceptualized the study, performed the investigation, and wrote and revised the manuscript.

### Data and Code Availability

Data are available from the Dryad Digital Repository (<https://doi.org/10.5061/dryad.m37pvmd5n>; Bush and Clayton 2022). Data underlying all figures and tables are provided.

### Literature Cited

- Amador, G. J., and D. L. Hu. 2015. Cleanliness is next to godliness: mechanisms for staying clean. *Journal of Experimental Biology* 218:3164–3174.
- Bateson, P., and K. N. Laland. 2013. Tinbergen's four questions: an appreciation and an update. *Trends in Ecology and Evolution* 28:712–718.
- Borchelt, P. L. 1980. Care of the body surface (COBS). Pages 363–384 in M. R. Denny, ed. *Comparative psychology: an evolutionary analysis of animal behavior*. Wiley, New York.
- Burnham, K. P., and D. R. Anderson. 2002. *Model selection and multi-model inference: a practical information-theoretic approach*. Springer, New York.
- Bush, S. E., and D. H. Clayton. 2018. Anti-parasite behaviour of birds. *Philosophical Transactions of the Royal Society B* 373:20170196.
- . 2022. Data from: Grooming time predicts survival in American kestrels. *American Naturalist*, Dryad Digital Repository, <https://doi.org/10.5061/dryad.m37pvmd5n>.
- Clayton, D. H., S. E. Bush, and K. P. Johnson. 2015. *Coevolution of life on hosts: integrating ecology and history*. University of Chicago Press, Chicago.
- Clayton, D. H., and P. Cotgreave. 1994. Relationship of bill morphology to grooming behaviour in birds. *Animal Behaviour* 47:195–201.
- Clayton, D. H., J. A. H. Koop, C. W. Harbison, B. R. Moyer, and S. E. Bush. 2010. How birds combat ectoparasites. *Open Ornithology Journal* 3:41–71.
- del Hoyo, J., A. Elliott, and J. Sargatal, eds. 1994. *Handbook of the birds of the world*. Vol. 2. New World vultures to guineafowl. Lynx, Barcelona.
- Fallon, S. M., E. Bermingham, and R. E. Ricklefs. 2005. Host specialization and geographic localization of avian malaria parasites: a regional analysis in the Lesser Antilles. *American Naturalist* 165:466–480.
- Goodman, G. B., M. C. Klingensmith, S. E. Bush, and D. H. Clayton. 2020. The role of scratching in the control of ectoparasites on birds. *Auk* 137:1–9.

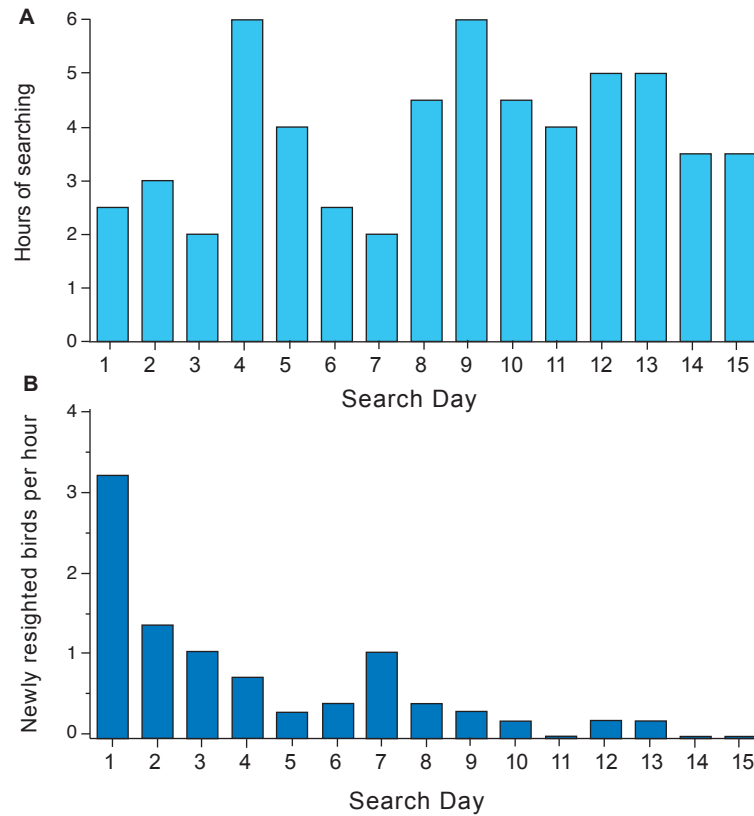
- Hallet, B. 2006. Birds of the Bahamas and the Turks and Caicos Islands. Macmillan Caribbean, Oxford.
- Hinnebusch, D. M., J. F. Therrien, M. A. Valiquette, B. Robertson, S. Robertson, and K. L. Bildstein. 2010. Survival, site fidelity, and population trends of American Kestrels wintering in southwestern Florida. *Wilson Journal of Ornithology* 122:475–483.
- Kalueff, A. V., J. L. La Porte, C. L. Bergner, eds. 2010. *Neurobiology of grooming behavior*. Cambridge University Press, Cambridge.
- Kass, L., T. Snyder, and K. Snyder. 2018. Updated list of endemic seed plant species found on San Salvador Island, the Bahamas, with a perspective on historical and current significance. *Caribbean Naturalist Special Issue* 2:48–75.
- Langlois, I. 2021. Medical causes of feather damaging behavior. *Veterinary Clinics* 24:119–152.
- Lebreton, J. D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* 62:67–118.
- Lewis, S., G. Roberts, M. P. Harris, C. Prigmore, and S. Wanless. 2007. Fitness increases with partner and neighbour allopreening. *Biology Letters* 3:386–389.
- Madden, K., and M. Mitchell. 2018. Case study: the use of falconry techniques in raptor rehabilitation. *Journal of Wildlife Rehabilitation* 38:7–10.
- Miller, J. R. 1978. Notes on birds of San Salvador Island (Watlings), the Bahamas. *Auk* 95:281–287.
- Moreno-Rueda, G. 2017. Preen oil and bird fitness: a critical review of the evidence. *Biological Reviews* 92:2131–2143.
- Nelson, B. C., and M. D. Murray. 1971. The distribution of *Mallophaga* on the domestic pigeon (*Columba livia*). *International Journal of Parasitology* 1:21–29.
- Nesse, R. M. 2013. Tinbergen's four questions, organized: a response to Bateson and Laland. *Trends in Ecology and Evolution* 28:681–82.
- Newton, I., M. J. McGrady, and M. K. Oli. 2016. A review of survival estimates for raptors and owls. *Ibis* 158:227–248.
- Newton-Fisher, N. E. 2021. *Animal behaviour pro*. Mobile app, version 1.6. <https://research.kent.ac.uk/lprg/software/>.
- Paulson, D. R. 1966. New records of birds from the Bahama Islands. *Philadelphia Academy of Natural Sciences* 394:1–15.
- Peig, J., and A. J. Green. 2009. New perspectives for estimating body condition from mass/length data: the scaled mass index as an alternative method. *Oikos* 118:1883–1891.
- Price, R. D., R. A. Hellenthal, R. L. Palma, K. P. Johnson, and D. H. Clayton. 2003. The chewing lice: world checklist and biological overview. *Natural History Survey Special Publication* 24. Illinois Natural History Survey, Champaign, IL.
- Sachs, B. D. 1988. The development of grooming and its expression in adult animals. *Annals of the New York Academy of Sciences* 525:1–17.
- Simmons, K. E. L. 1985. Comfort behaviour. Pages 101–105 in B. Campbell and E. Lack, eds. *A dictionary of birds*. Buteo, Vermillion, SD.
- Smallwood, J. A., and D. M. Bird. 2020. American kestrel (*Falco sparverius*), version 1.0. In A. F. Poole and F. B. Gill, eds. *Birds of the world*. Cornell Lab of Ornithology, Ithaca, NY. <https://doi.org/10.2173/bow.amekes.01>.
- Smith, R. R. 1993. *Field guide to the vegetation of San Salvador Island, the Bahamas*. 2nd ed. CCFL Bahamian Field Station, San Salvador.
- Spuijdt, B. M., J. A. Van Hooff, and W. H. Gispen. 1992. Ethology and neurobiology of grooming behavior. *Physiological Reviews* 72:825–852.
- Tinbergen, N. 1963. On the aims and methods of ethology. *Zeitschrift für Tierpsychologie* 20:410–463.
- van der Marel, A., C. L. O'Connell, S. Prasher, C. Carminito, X. Francis, and E. A. Hobson. 2021. A comparison of low-cost behavioral observation software applications for handheld computers and recommendations for use. *Ethology* 128:275–284. <https://doi.org/10.1111/eth.13251>.
- Villa, S. M., H. E. Campbell, S. E. Bush, and D. H. Clayton. 2016. Does anti-parasite behavior improve with experience? an experimental test of the priming hypothesis. *Behavioural Ecology* 27:1167–1171.
- White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46: S120–S139.
- Williams, B. K., J. D. Nichols, and M. J. Conroy. 2002. *Analysis and management of animal populations*. Academic Press, San Diego, CA.
- Yanagawa, A., W. Huang, A. Yamamoto, A. Wada-Katsumata, C. Schal, and T. F. Mackay. 2020. Genetic basis of natural variation in spontaneous grooming in *Drosophila melanogaster*. *G3: Genes, Genomes, Genetics* 10:3453–3460.
- Yorinks, N., and C. T. Atkinson. 2000. Effects of malaria on activity budgets of experimentally infected juvenile Apapane (*Himatione sanguinea*). *Auk* 117:731–738.
- Zhang, Y. F., L. Vargas Cifuentes, K. N. Wright, J. P. Bhattarai, J. Mohrhardt, D. Fleck, and E. Janke. 2021. Ventral striatal islands of Calleja neurons control grooming in mice. *Nature Neuroscience* 24:1699–1710. <https://doi.org/10.1038/s41593-021-00952-z>.
- Zhukovskaya, M., A. Yanagawa, and B. T. Forschler. 2013. Grooming behavior as a mechanism of insect disease defense. *Insects* 4:609–630.

**Supplement to**  
**Grooming time predicts survival:**  
**American kestrels, *Falco sparverius*, on a sub-tropical island**

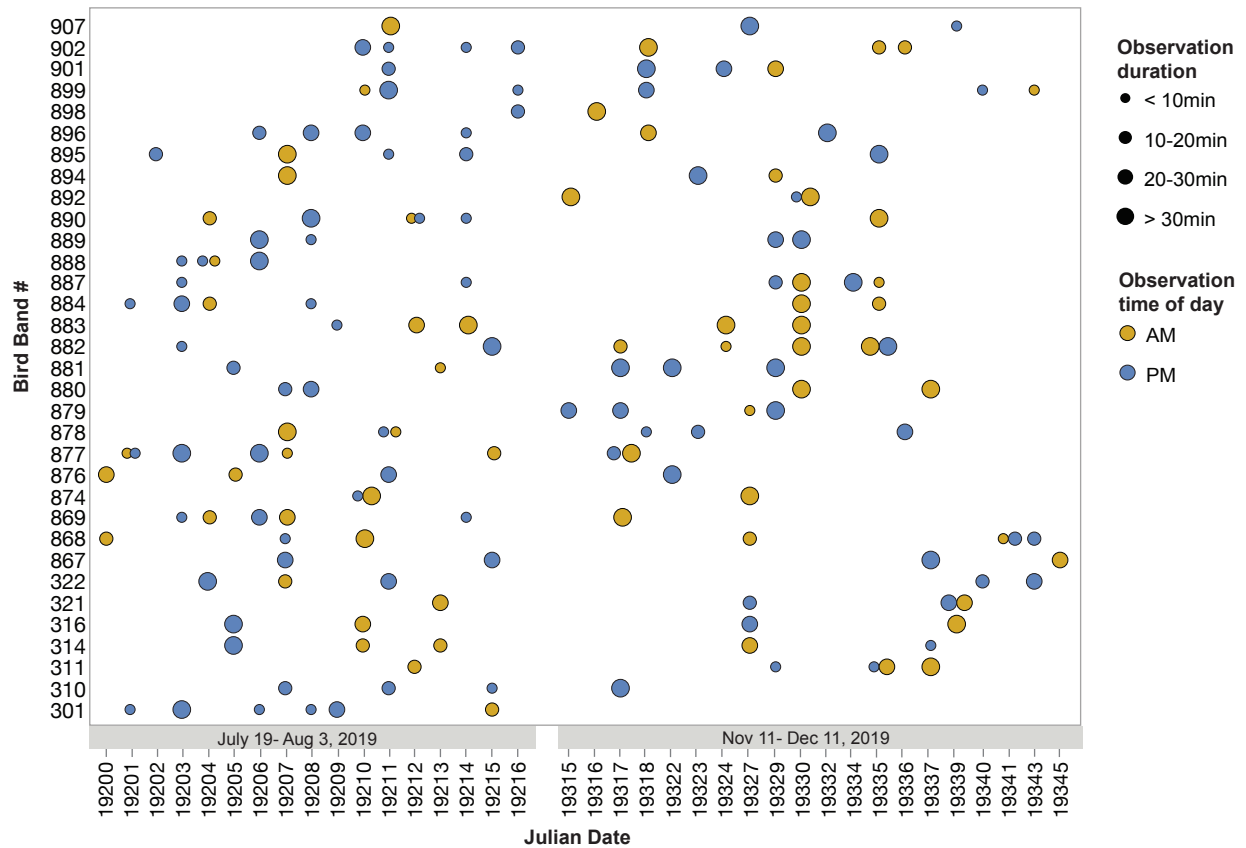
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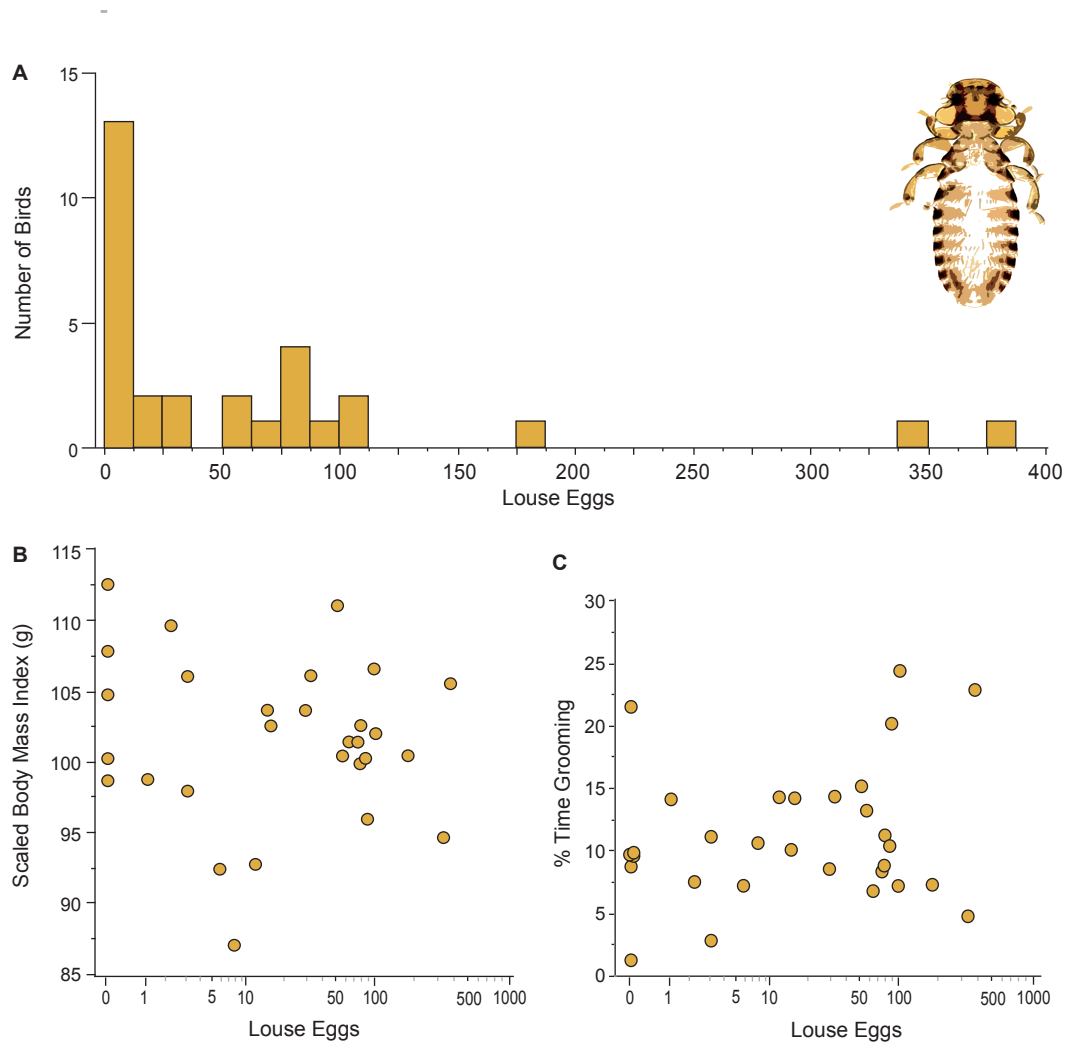
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**Figure S1. (A)** Hours spent searching for banded kestrels in July, 2021, at the end of the study. **(B)** Newly resighted birds per hour of searching; e.g. 8 birds were newly resighted during 2.5 hours of searching on Day 1. No birds were newly resighted during 3.5 hours of searching on Day 14 or again on Day 15.



**Figure S2.** Distribution of behavioral observations over time. Behavioral data for each bird (y-axis) was collected over several occasions that varied in duration (point size), time of day (point color), and date and season (x-axis).



**Figure S3.** (A) Distribution of *Colpocephalum subzerafae* louse egg abundance among 30 kestrels. Eggs were found on 26 of the birds (87%); the first bar represents 13 birds with 0-12 eggs each (one wing). Inset: illustration of *Colpocephalum* from a museum specimen. (B) Relationship of body condition to *C. subzerafae* louse egg abundance ( $R^2 = 0.02$ ,  $P = 0.46$ ). (C) Relationship of grooming time to louse egg abundance ( $R^2 = 0.05$ ,  $P = 0.25$ ).