

Birds groom more in regions with higher parasite pressure: a comparison of temperate and subtropical American kestrels

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Grooming behaviour, which maintains and cleans the integument, is a widespread behaviour of birds, mammals and arthropods. The extent to which grooming is influenced by large-scale environmental differences, such as geographical and seasonal variation, remains largely unexplored. We investigated spatial and temporal variation in the grooming behaviour of a common species of bird, the American kestrel, *Falco sparverius*. Specifically, we compared the self-grooming behaviour (preening and scratching) of kestrels in the subtropical Bahamas to kestrels in temperate northern Utah, U.S.A., in both summer and winter. We also compared differences in parasite 'pressure' by quantifying the prevalence and abundance of ectoparasitic lice (Insecta: Phthiraptera) on kestrels in both locations. Bahama kestrels had significantly more lice than Utah kestrels, which is typical of birds in humid regions, compared to arid regions. Bahama kestrels groomed significantly more than Utah kestrels, which may constrain the time–activity budgets of Bahama kestrels. Within each region, however, birds with more lice did not groom more. This pattern is consistent with geographical differences in programmed grooming, rather than stimulus-driven grooming. Kestrels in both locations groomed significantly more in summer than in winter, presumably because feather moult occurs in summer. To our knowledge, this study provides the first demonstration of geographical variation in the grooming behaviour of any animal. Experimental studies are needed to confirm the causes and consequences of this variation. Spatial and temporal comparisons of grooming in other birds, as well as mammals and arthropods, would be informative.

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Grooming behaviour, which helps maintain and clean the integument, is a widespread behaviour of arthropods, birds and mammals, including humans (Amador & Hu, 2015; Clayton et al., 2010; Kupfer & Fessler, 2018; Spruijt et al., 1992; Zhukovskaya et al., 2013). Despite its obvious importance, the adaptive function and evolution of grooming has received surprisingly little attention, compared to foraging, navigation, parenting and many other aspects of animal behaviour. Understanding the adaptive basis of grooming requires exploration of how it varies among individuals, populations and species and how that variation is influenced by different ecological circumstances. The goal of the current study was to compare the grooming rates of populations of birds

living in different geographical regions and in different seasons of the year.

Avian grooming has two components: preening with the beak (Fig. 1) and scratching with the feet (Cantarero et al., 2013; Christie et al., 1996; Clayton, 1991; Dowling et al., 2001; Tripet et al., 2002). Preening occurs when a bird pulls one or more feathers between the mandibles of the beak or nibbles feathers with the tips of the beak (Bush & Clayton, 2018). Preening functions to clean and arrange feathers, 'zip' the barbules of flight feathers together, distribute preen oil and powder down and control ectoparasites (Clayton et al., 2010; Jenni & Winkler, 2020; Roulin et al., 2016). Preening can also serve as displacement behaviour (Henson et al., 2012; Rowell, 1961; Tinbergen, 1952) and it has been ritualized as part of courtship display in some groups (McKinney, 1965; Tinbergen, 1952).

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Figure 1. The most common form of grooming in birds is preening with the beak, as illustrated by this female American kestrel preening a tail feather (Photo credit: PDMPHOTOS, photos@paulmoulton.com).

The second component of avian grooming, scratching with the feet, controls ectoparasites on the head and neck by flushing them to lower regions of the body, where they can be removed by preening (Goodman et al., 2020). Scratching also relieves itching and helps distribute oil on the head feathers after birds have transferred preen oil from the beak to the feet (Simmons, 1961, 1985). Scratching requires more coordination than preening, which is why it is one of the last behaviours to develop in nestling birds, while preening is one of the first behaviours to develop (Horwich, 1969).

Allopreening, preening of one bird by another, is a form of social grooming that, like scratching, can help control ectoparasites on regions that cannot be self-preened, such as the head and neck (Brooke, 1985; Villa, Goodman, et al., 2016). Allopreening also plays an important role in mediating social interactions (Gill, 2012; Kenny et al., 2017; Lewis et al., 2007; Radford & Du Plessis, 2006; Roulin et al., 2016), similar to the social role of allogrooming in mammals (Duboscq et al., 2016a; 2016b) and social insects (Richard & Hunt, 2013; Zhukovskaya et al., 2013). All species of birds preen, but only some species allopreen (Kenny et al., 2017).

Grooming requires time and energy that cannot be devoted to other activities. Overall, birds average about 8.5% of their time grooming (Cotgreave & Clayton, 1994; Walther & Clayton, 2005). This investment is much higher in some species, such as common loons, *Gavia immer*, which devote up to 25% of their time to grooming (Daub, 1989; McIntyre, 1978). Preening accounts for more than 90% of grooming behaviour in most species of birds (Walther & Clayton, 2005). The energetic cost of preening ranges from 1.6 to 2.3 times basic metabolic rate (Goldstein, 1988). Croll and McLaren (1993) documented a 196% increase above resting metabolic rate in thick-billed murre, *Uria lomvia*, during preening compared to increases of only 49% for feeding and 140% for diving.

Grooming also appears to have other costs. Preening reduces vigilance, which may lead to increased predation and competition (Beauchamp & Ruxton, 2003; Randler, 2005; Redpath, 1988). Preening also increases the risk of infectious disease, at least in aquatic environments, where influenza viral particles are concentrated in preen oil, then potentially ingested during preening and

allopreening (Delogu et al., 2010). Preen oil is also thought to be physiologically costly to produce (Moreno-Rueda, 2017). These costs, in addition to the time and energy required for grooming, may generate fitness trade-offs between time spent grooming and other activities, such as foraging.

Bush and Clayton (2023) recently showed that time spent grooming varies among individuals and that this variation is a strong predictor of fitness. The authors collected data on the grooming time and survival of a population of American kestrels, *Falco sparverius*, on San Salvador Island, Bahamas. The data revealed a quadratic relationship between grooming time and survival over a period of 2 years, consistent with stabilizing selection on grooming time. Kestrels on the island spent 1.2–30.4% of their time grooming. With the exception of a single bird that groomed 21% of the time, all surviving kestrels groomed an intermediate amount (7–15%) of time; birds that groomed more or less than this amount had significantly reduced survival rates.

Grooming is a constitutive, centrally programmed behaviour performed on a regular basis by birds and other animals (Fentress, 1988; Mooring et al., 2004; Ravbar et al., 2021; Spruijt et al., 1992). Grooming also has an inducible component that responds to environmental stimuli, such as changes in ectoparasite pressure (Hawlana et al., 2008; Mooring et al., 1996; Villa, Campbell, et al., 2016). Brown (1974) showed that poultry experimentally infested with lice groom 5–10 times more than control birds with smaller numbers of lice. Similarly, pigeons experimentally infested with lice groom about a third more than control birds without lice (Villa, Campbell, et al., 2016). In contrast, the extent to which grooming may be influenced by large-scale environmental differences, such as geographical or seasonal variation, is unknown, at least in birds (see Duboscq et al., 2016a, 2016b, for effects of season on grooming by social primates).

The goals of the current paper were to test for large-scale spatial effects (geographical region), seasonal effects and effects of differences in ectoparasite pressure on the grooming ecology of American kestrels, which are distributed throughout North America and the Caribbean. We quantified and compared the grooming behaviour of kestrels in the subtropical Bahamas to the grooming behaviour of kestrels in temperate northern Utah, U.S.A. We collected data in both the summer and winter seasons to test the influence of season on grooming behaviour. None of the birds in our study engaged in social grooming (allopreening); we observed only self-grooming.

We also collected data on the ectoparasite loads of kestrels in both locations. Control of ectoparasites, such as chewing lice (Insecta: Phthiraptera), is an important function of grooming (Bush & Clayton, 2018; Clayton et al., 2010, 2015). Ectoparasites are one of the best documented stimuli triggering an increase in the grooming rates of birds (Brown, 1974; Cantarero et al., 2013; Villa, Campbell, et al., 2016; Waite et al., 2012), as well as mammals (Hawlana et al., 2008; Mooring et al., 1996). Chewing lice of birds reduce host fitness through their effects on survival, host mating success and other aspects of host reproductive biology (Clayton et al., 2008, 2015).

METHODS

San Salvador, Bahamas

Kestrels on San Salvador Island are members of the nonmigratory subspecies *Falco sparverius sparveroides* that is endemic to the Bahamas, Cuba and the Isle of Pines (del Hoyo et al., 1994). The North American subspecies *F. s. sparverius*, which is migratory and winters on some of the northern Bahama islands, does not occur on San Salvador (Hallet, 2006; Miller, 1978; Paulson, 1966; S. E. Bush &

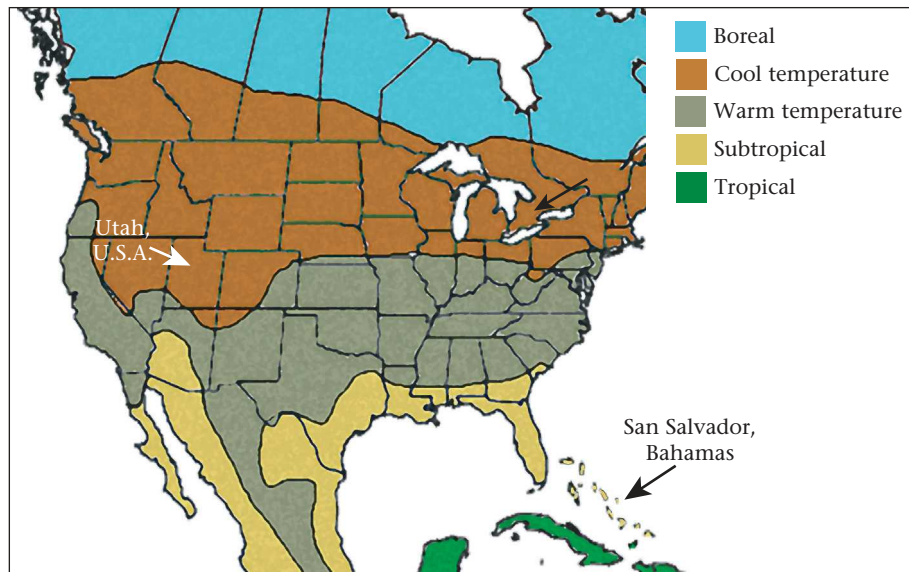


Figure 2. Map with study sites (redrawn from Sayre et al., 2020). Mean annual temperature ranges from -6°C to 31°C in northern Utah and from 23°C to 29°C in the Bahamas. Mean low ambient humidity is 36% in northern Utah and 74% in the Bahamas (WorldWeatherOnline.com). White arrow indicates northern Utah; black arrow indicates San Salvador Island.

D. H. Clayton, personal observations). San Salvador (Fig. 2) is located along the eastern edge of the Bahama Archipelago (24°N , $74^{\circ}30'\text{W}$). The island is small (~ 20 km long, ~ 11 km wide), with an area of ~ 157 km². We conducted fieldwork in 2019 in two bouts, a summer season (19 July–4 August) and a winter season (11 November–11 December), each designed to avoid the mid-August–October rainy season. We used Bal-chatri traps to capture kestrels in the summer to band them for individual identification and again in the winter to quantify parasite loads (see below). Upon capture, we fitted each bird with a falconry hood to minimize stress (Madden & Mitchell, 2018) and banded each bird with a unique combination of colour bands and a numbered band. Upon release at the capture site, some birds pulled at their bands for several hours or days after banding, but most birds soon ignored their bands.

Northern Utah U.S.A.

Utah kestrels are members of the nominate subspecies *F. s. sparverius*, which is a partial migrant, with larger proportions of northern populations migrating and southern populations tending to be sedentary (Goodrich & Smith, 2008; Ruegg et al., 2021). We conducted Utah fieldwork in 2020–2021 during two bouts: summer (4 June–28 July 2020) and winter (13 November 2020–18 February 2021). In contrast to the year-round resident Bahama population, northern Utah populations of kestrels are made up largely of different birds in summer versus winter. In summer we collected data from a breeding population of colour-banded kestrels that were part of HawkWatch International's long-term demographic studies of kestrels in northern Utah. In winter we colour-banded and observed kestrels that were presumably short-distance winter migrants; kestrels in middle latitudes

(44 – 36°N), such as Utah, move relatively short distances in response to local weather-related prey availability (Smallwood & Bird, 2002). This probably explains why only 1 of 16 Utah summer birds (Table 1) was resighted in the winter (only summer data from this single bird were used for analysis; see below).

Grooming Behaviour

We collected data on the grooming behaviour of kestrels with focal animal sampling (Altmann, 1974), while observing birds through binoculars or spotting scopes and recording behaviour with the Animal Behaviour Pro App for iPhone (Newton-Fisher, 2021; van der Marel, 2021). We recorded the behaviour of each bird until it flew out of sight. Observation periods varied in duration (Appendix, Figs A1–A2). In total, we collected a minimum of 30 min of data that included both morning and afternoon observations (Appendix, Figs A1–A2). On average, we had three observation periods per bird (range 2–6). During each observation period, we monitored the proportion of time birds spent grooming (preening and scratching). Each bout of grooming ended when a bird stopped for more than 3 s or switched to a different behaviour (Clayton & Cotgreave, 1994). The proportion of time that each kestrel spent grooming was determined by calculating the total grooming time divided by the total observation time across all observation periods. The method of data collection was consistent across geographical regions (Bahamas versus Utah) and seasons.

Parasites

We collected ectoparasite data in two stages: the first qualitative and the second quantitative (Clayton & Drown, 2001; Clayton &

Table 1
Sample sizes of kestrels providing behavioural and/or parasite data

	Behaviour data <i>N</i> (♀, ♂)	Parasite data <i>N</i> (♀, ♂)	Behaviour and parasite data <i>N</i> (♀, ♂)
Bahamas summer	18 (13♀, 5♂)	—	—
Bahamas winter	32 (17♀, 15♂)	68 (45♀, 23♂)	34 (18♀, 16♂)
Utah summer	16 (10♀, 6♂)	—	—
Utah winter	26 (14♀, 12♂)	50 (23♀, 27♂)	27 (14♀, 13♂)
Total	92 (54♀, 38♂)	118 (68♀, 50♂)	61 (32♀, 29♂)

Walther, 1997). In the first stage, each bird was trapped and held on its back in one hand while we spent about 5 min searching for adult lice by deflecting feathers of the throat (gulum), breast, belly and cloacal region (crissum) with a pair of forceps. We did not closely examine feather tracts with tightly packed feathers, such as the back, because deflecting those feathers would risk breaking them. The goal of this first stage was to collect voucher specimens of chewing lice for identification, but the majority of lice were left on the birds. Voucher specimens were identified by microscopic examination and reference to Price et al. (2003). In the Bahamas, we found two species of lice: *Degeeriella carruthi* (Ischnocera) and *Colpocephalum subzerafae* (Amblycera); voucher specimens of both species are deposited in the Price Institute of Parasite Research, University of Utah (PIPRO20001 and PIPRO20002) and are digitally accessible via <https://scan-bugs.org>. In Utah, we found one species of chewing louse: *C. subzerafae*. No other ectoparasites (insects, mites or ticks) were found on any of the kestrels in the study, despite careful visual examination (Clayton & Drown, 2001; Clayton & Walther, 1997).

The second stage of data collection involved careful quantification of the eggs of chewing lice, which are 'permanent' parasites that complete their entire life cycle on the body of the host (Clayton et al., 2015). The eggs, which are about 0.6 mm long, were observed under a dissecting microscope (see below) and used as a proxy for overall louse load. Lice glue their eggs to feathers with a glandular cement. Like other members of the genus *Colpocephalum* (Nelson & Murray, 1971), *C. subzerafae* glues its eggs between feather barbs on the underside of flight feathers of the wing (primaries 1–6 and secondaries 1–3). When the egg hatches, its top (operculum) pops off like a cap, leaving most of the empty shell behind, where it remains attached to the feather (Clayton et al., 2015). The number of hatched (and unhatched) eggs on a feather provide a cumulative record of the number of eggs laid over the life of that feather. The annual feather moult for kestrels begins in the spring (Smallwood & Bird, 2002). Thus, egg counts in our study provide a longitudinal index of the number of lice on a bird over many months, including summer and autumn.

At each study site, a single researcher counted *C. subzerafae* eggs (hatched and unhatched) on the primary and secondary flight feathers of one wing of captured kestrels using a stereomicroscope. Eggs of the second species of louse, *D. carruthi*, were not counted because their attachment site is unknown. We did not wish to unduly disturb the kestrels by searching through their plumage to find the location of *D. carruthi* eggs.

Statistical Methods

We used beta regression to analyse the influence of geographical location, season, sex, observation time, the interaction between season and sex and the interaction between season and location on the proportion of time kestrels spent grooming. Parasite abundance was not included as a covariate in the overall models because the parasite data were restricted to winter; analyses of parasite data were conducted in separate models (see below). Our estimates of grooming time were calculated as a proportion of total observation time; however, continuous proportional data often violate assumptions of standard statistical techniques, which assume that error terms are normally distributed and have constant variance (Douma & Weedon, 2019). Beta regression circumvents these assumptions by estimating parameters for both mean (μ) and precision (ϕ) (Simas et al., 2010). We used a variable ϕ model (Douma & Weedon, 2019) to account for potential differences in the precision of our estimates of grooming time among different seasons and locations and across different observation times. Similar to GLMs with logit transformations, the fitting algorithms for beta

regression can only handle proportions on the open interval (0,1), so grooming time was linearly rescaled prior to modelling (Douma & Weedon, 2019). We had a total of 98 estimates of grooming time from 92 birds (five Bahama birds and one Utah bird were observed in both summer and winter). To avoid pseudoreplication, we included only the first estimate for each of these six birds, for a total of 92 estimates of grooming time from 92 birds (Table 1, Behaviour data). For analyses involving parasites (Table 1, Behaviour and parasite data), we used winter behavioural data because the parasite data were collected in the winter.

Location, season, sex, the interaction between location and season and the interaction between season and sex were modelled as fixed effects on mean grooming time (μ). Location, season, observation time and the interaction between location and season were modelled as fixed effects on precision (ϕ). We included an interaction term for sex and season because grooming time may vary seasonally between male and female kestrels; for example, male kestrels may groom more in winter to appear more attractive to potential mates at the start of the breeding season. We also included an interaction term for location and season because the influence of season on grooming time may vary between locations with different climatic variation (seasonal temperature typically varies by 37°C in Utah but only by 6°C in the Bahamas; Fig. 2). The saturated model was constructed with all the covariates for both μ and ϕ as described above. Nonsignificant variables were removed from the saturated model by backward elimination to find the minimal model. A null model was constructed where μ was modelled as a constant with variable precision.

We tested for a relationship between louse abundance and grooming time using winter behavioural data because all parasite data were collected in winter. Analyses of louse abundance and grooming time were conducted separately for birds in Utah and the Bahamas because louse load differed dramatically between the two regions (see Results). In total, our beta regression analyses included the 34 Bahama kestrels and 27 Utah kestrels for which we had at least 30 min of behavioural data (as described above) and parasite data (Table 1). Louse abundance was transformed ($\log + 1$) to normalize these data prior to analysis with beta regression. Louse abundance, sex and the interaction between louse abundance and sex were modelled as fixed effects on mean grooming time (μ). Observation time was modelled as a fixed effect on precision (ϕ). We included an interaction term for sex and louse abundance because male and female kestrels may groom different amounts in response to the same level of parasitism. The saturated model for the Bahamas was constructed with all the covariates for both μ and ϕ , as described above. The saturated model for Utah was constructed with all but one of the covariates for both μ and ϕ , as described above; an interaction term for sex and louse abundance was not included in this model because only three of the 27 Utah kestrels had lice (see Results). Null models were constructed where μ was modelled as a constant with variable precision.

We used Akaike information criterion (AIC) scores to evaluate the differences in model fit for all beta regression models. All maximum likelihood parameter estimates were adjusted using bias correction (Kosmidis & Firth, 2010). The significance of coefficient parameter estimates was calculated from partial Wald tests. Beta regression models were implemented using the 'betareg' package (version 3.1–4; Cribari-Neto & Zeileis, 2010) in R (version 4.2.2; R Core Team, 2023).

Ethical Note

Kestrels were trapped using Bal-chatri traps, which are harmless to kestrels. The trap was placed beneath a perched kestrel and watched continuously until the bird was trapped, at which point

the bird was removed from the trap within 1–2 min and fitted with a falconry hood to minimize stress (Madden & Mitchell, 2018). Hooded birds were placed in a dark bag during transport which, again, minimized stress. They remained hooded during the process of banding, measuring and searching for ectoparasites (as described above). Birds were usually released within 3 h of capture. Handling of birds in the Bahamas was performed in accordance with a 2019 permit from the Bahamas Environment, Science and Technology Commission (Ministry of the Environment), as well as the Institutional Animal Care and Use Committee of the University of Utah (IACUC protocol 17-03012). Handling of birds in Utah was performed in accordance with a Utah Certificate of Registration (1BAND2199), U.S. federal banding permits 21384 and 24077 and the Institutional Animal Care and Use Committee of the University of Utah (IACUC protocol 20-10007).

RESULTS

Grooming

The mean ($\pm$ SE) quantity of behavioural data per bird was 50.5 ± 2 min, with a minimum of 30.2 min and a maximum of 121.7 min. Overall, kestrels spent a mean of 7.45% of their time grooming, divided between preening (85.4%) and scratching (14.6%). Kestrels were never observed to allopreen; all preening was self-preening.

Bahama kestrels spent a mean ($\pm$ SE) of $15.0 \pm 2.1\%$ of their time grooming in summer, compared to a mean of $5.9 \pm 1.1\%$ in winter (Fig. 3). Utah kestrels spent a mean of $9.8 \pm 1.8\%$ of their time grooming in summer, compared to a mean of $2.7 \pm 0.7\%$ in winter.

Location and season each had a significant effect on grooming time (Table 2). Kestrels in the Bahamas devoted significantly more time to grooming than kestrels in Utah ($P = 0.006$). Kestrels also spent significantly more time grooming in summer than in winter ($P < 0.001$). In contrast, sex was not a significant predictor of grooming ($P = 0.436$). The interaction between location and season was not significant ($P = 0.709$), and the interaction between sex and season was not significant ($P = 0.721$; Table 2). Both the saturated and minimal models provided a better fit than the null model

(Δ AICs > 32). The minimal model was the most parsimonious model with the lowest AIC score (Table 2). The mean proportion of grooming time was best explained by location and season, while precision in grooming time was best explained by observation time and season.

Parasites

Parasites often show an aggregated distribution, with most hosts having few parasites, while a few hosts have many (Poulin, 2011). For this reason, accurate quantification of parasite abundance depends on large host sample sizes (Galloway & Lamb, 2021). We collected parasite data from a total of 68 kestrels in the Bahamas and 50 kestrels in Utah (Table 1).

In the Bahamas, eight kestrels (11.8%) had one to three *Colpocephalum subzerafae* lice and 40 kestrels (58.8%) had *C. subzerafae* eggs. Infested birds had 1–384 eggs (Fig. 4a). Six kestrels (8.8%) had 1–12 *Degeeriella carruthi* lice but no eggs of this species were observed (see Methods). Two of the kestrels with *D. carruthi* were co-infested with *C. subzerafae* eggs. In Utah, only six kestrels (12.0%) had *C. subzerafae* eggs (range 4–19 eggs) (Fig. 4a). No hatched lice of either species were observed on any of the Utah kestrels.

Overall prevalence of lice on Bahama kestrels (58.8%) was significantly higher than overall prevalence of lice on Utah kestrels (12.0%) (Fisher's exact: $N = 118$, $P < 0.0001$; Fig. 4b). Lice were also significantly more abundant in the Bahamas (Wilcoxon: $Z = -5.3$, $N = 118$, $P < 0.001$). Bahama kestrels had a mean ($\pm$ SE) of 40.8 ± 8.6 lice, while Utah kestrels had a mean of only 1.4 ± 0.6 lice (Fig. 4c).

Louse abundance, host sex and the interaction between louse abundance and host sex were not significant predictors of grooming time in Bahama kestrels ($P > 0.05$; Table 3). Similarly, there was no significant relationship between grooming time and louse abundance or sex in Utah kestrels ($P > 0.05$; Table 3). No parameter estimates besides the intercepts were significant predictors of grooming time in the saturated models. The null models for grooming and parasite pressure for both the Bahama and Utah kestrels were the best-fit models, based on AIC scores (Table 3).

DISCUSSION

We investigated the influence of geographical location, season, sex and parasite abundance on the grooming time of American kestrels. We also tested for interactions between season and sex, season and location, and sex and parasite abundance. To our knowledge, this is the first study to test for geographical variation in time spent grooming. Our results show that, regardless of season, kestrels in the Bahamas groom more than kestrels in Utah. In summer, Bahama kestrels groomed 50% more than Utah kestrels; in winter, Bahama kestrels groomed about twice as much as Utah kestrels (Fig. 3). Our results also show seasonal differences in grooming. Bahama kestrels groomed nearly three times more in summer than in winter (Fig. 3), and Utah kestrels groomed nearly four times more in summer than in winter. To our knowledge, this result is one of the first demonstrations of seasonal differences in grooming. Sex did not correlate with grooming time either as a main effect or in interactions with louse abundance or location. Below we consider hypotheses explaining geographical differences in grooming, such as differences in parasite abundance, followed by hypotheses explaining seasonal differences in grooming.

The higher rate of grooming in Bahama kestrels parallels higher parasite pressure in the Bahamas (Fig. 4), despite a lack of association between time spent grooming and parasite abundance among birds within the Bahamas (Fig. 5a). The greatest within-region variation in grooming was observed among birds without

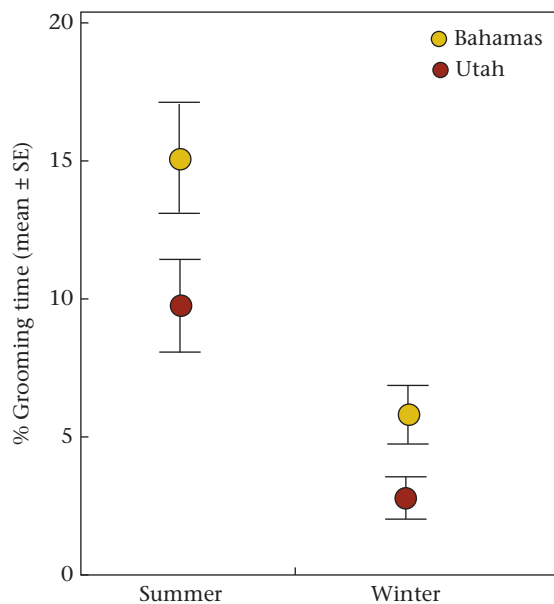


Figure 3. Grooming time of kestrels in different locations and seasons (also see Table 2).

Table 2
Maximum likelihood parameter estimates (standard error) of beta regressions investigating the relationships between geographical location, season, host sex and grooming time

Model	Intercept	Location (Utah)	Season (winter)	Location × season	Sex (male)	Sex × season	AIC
Mean grooming time (μ)							
Null model	−2.34*** (0.10)	—	—	—	—	—	−279.29
Saturated model	−1.60*** (0.16)	−0.49* (0.24)	−1.07*** (0.23)	−0.13 (0.33)	−0.18 (0.23)	0.11 (0.31)	−312.01
Minimal model	−1.69*** (0.12)	−0.41** (0.15)	−1.08*** (0.16)	—	—	—	−318.07
Model of precision (ϕ)							
Null model	1.21 (0.66)	0.66 (0.45)	0.51 (0.42)	−1.07 (0.55)	0.02* (0.01)	Observation duration	
Saturated model	0.86 (0.69)	0.40 (0.50)	0.90 (0.47)	0.15 (0.63)	0.03** (0.01)		
Minimal model	1.14* (0.57)	—	0.92** (0.34)	—	0.03** (0.01)		

Asterisks show significance of partial Wald tests: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

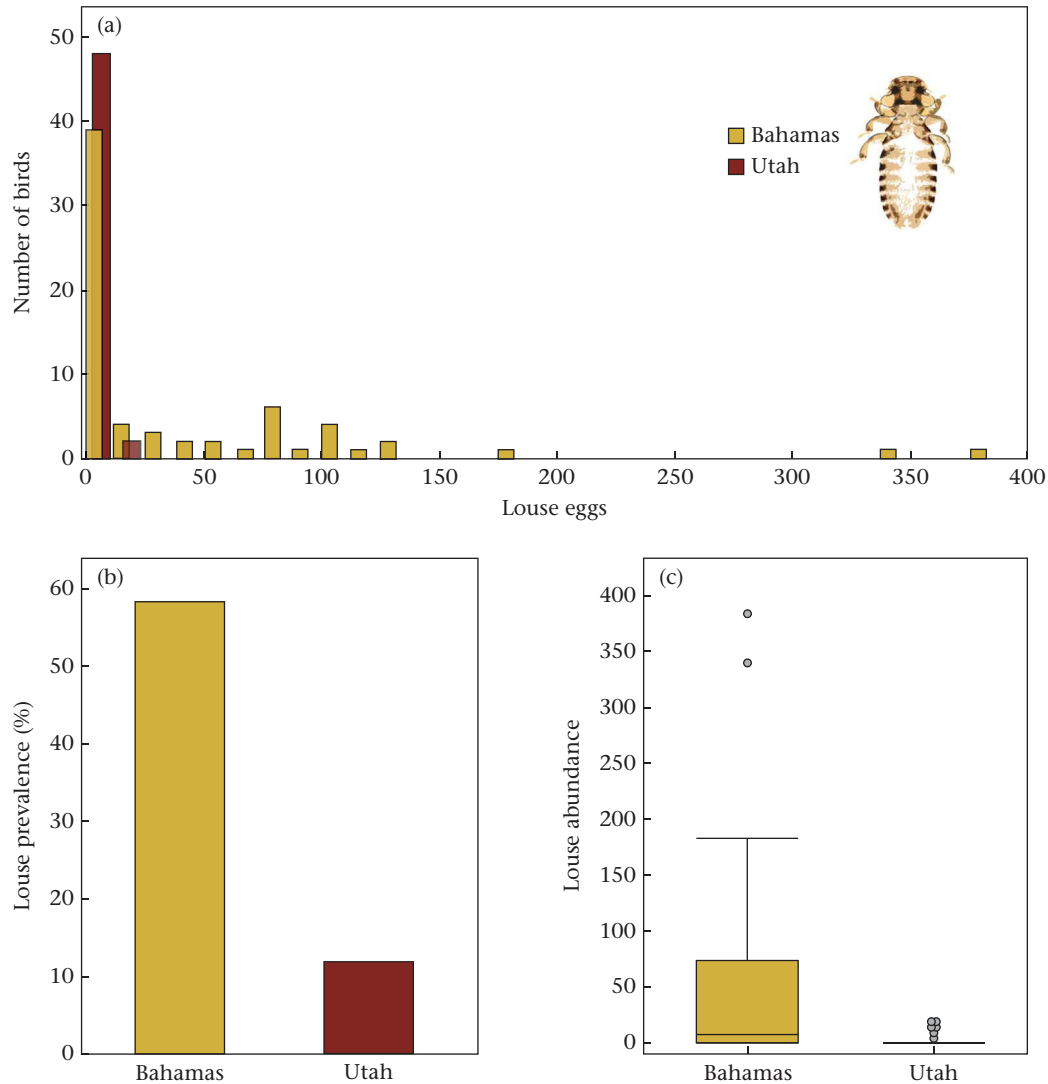


Figure 4. (a) Distribution of *Colpocephalum* eggs among kestrels examined for lice (one wing); illustration of *Colpocephalum* by S.E. Bush. (b) Prevalence of lice in different locations. (c) Abundance of lice in different locations.

any parasites, both in the Bahamas (Fig. 5a) and in Utah (Fig. 5b). The relationship between grooming and parasite pressure between regions, but not within region, may be a consequence of the fact that our data were correlative. Experimental increases in lice trigger increased grooming (Clayton et al., 2015; Goodman et al., 2020; Villa, Campbell, et al., 2016). Without an experimental manipulation, however, louse load and grooming can show

negative frequency dependence. More gradual increases in lice may trigger gradual increases in grooming, leading to decreases in lice, which in turn cause a decrease in grooming. Unless the dynamics of the lice and grooming are tightly linked, patterns such as those shown in Fig. 5 can result, particularly when indices of parasite load rely on cumulative egg counts. A more rigorous test of the effect of lice on grooming, within a region, requires experimental

Table 3

Maximum likelihood parameter estimates (standard error) of beta regressions investigating the relationships between grooming time, host sex and parasite pressure

Model	Intercept	Louse abundance	Sex (male)	Louse abundance $\times$ sex	AIC
Mean grooming time (μ)					
Bahamas null model	−2.75*** (0.74)	—	—	—	−121.77
Bahamas saturated model	−2.79*** (0.26)	0.04 (0.10)	0.11 (0.36)	−0.11 (0.14)	−115.98
Utah null model	−3.35*** (0.18)	—	—	—	−127.12
Utah saturated model	−3.33*** (0.24)	−0.01 (0.18)	−0.01 (0.30)	—	−122.82
Precision (ϕ)					
Bahamas null model	2.06*** (0.74)	0.02 (0.02)	—	—	—
Bahamas saturated model	1.90* (0.76)	0.02 (0.02)	—	—	—
Utah null model	2.90* (1.18)	0.02 (0.03)	—	—	—
Utah saturated model	2.81* (1.18)	0.02 (0.03)	—	—	—

Asterisks show significance of partial Wald tests: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

manipulation of louse abundance, with downstream monitoring of grooming (Brown, 1974; Villa, Campbell, et al., 2016).

The higher rate of grooming in the Bahamas, compared to Utah, may reflect an evolutionary difference in programmed grooming. The programmed grooming model assumes that grooming is driven by an internal timing mechanism that periodically evokes a bout of grooming independent of stimuli, such as parasites (Mooring & Samuel, 1998). Although kestrels in the Bahamas and Utah are members of the same species, they are well-differentiated populations that are members of different subspecies. These populations may have evolved different levels of programmed grooming in response to long-standing differences in the

ectoparasite loads of birds in humid versus arid regions (Bush et al., 2009; Clayton et al., 2015; Malenke et al., 2011; Moyer, Drown, & Clayton, 2002). Ambient humidity is much lower in Utah than in the Bahamas (Fig. 2). Ectoparasites, such as bird lice, are more common in humid regions because they depend on water extracted directly from the atmosphere (Rudolph, 1983). Plumage does not buffer humidity, which fluctuates near the skin of the host in response to differences in ambient humidity (Moyer, Drown, & Clayton, 2002). In contrast, ambient temperature has little effect on lice, which complete their entire life cycle on the body of the host, where the plumage does buffer them from dramatic changes in ambient temperature (Clayton et al., 2015). The extent to which regional differences in grooming are caused by evolutionary differences in programmed grooming could be tested using captive individuals held under identical common garden conditions.

It is possible that the higher rate of grooming in Bahama kestrels is caused by factors other than, or in addition to, differences in parasite pressure. For example, it is conceivable that birds in the Bahamas may need to preen more for better distribution of preen oil to keep plumage dry during heavy periods of subtropical rainfall. Preen oil is known to improve waterproofing, although it remains unclear whether it does this by creating a hydrophobic layer, or by improving the plumage structure (Moreno-Rueda, 2017). Unfortunately, no data are available regarding the distribution of preen oil by kestrels in the Bahamas or Utah. Similarly, no data exist with which to test for possible differences in the moult patterns of Bahama and Utah kestrels, which could also influence grooming time.

The results of this paper also demonstrate seasonal differences in grooming. Kestrels in the Bahamas groomed nearly three times more in summer than in winter (Fig. 3), and Utah kestrels groomed nearly four times more in summer than in winter. The higher rate of summer grooming coincides with the annual feather moult, which begins in spring and concludes by early autumn (Smallwood & Bird, 2002). Verbeek (1972) showed a similar increase in the grooming rates of moulting yellow-billed magpies, *Pica nuttalli*. During moult, preening is known to facilitate the emergence of mature feathers from developing pin feathers (Maderson et al., 2009). Similarly, scratching facilitates the emergence of mature feathers on regions that cannot be reached by preening, such as the head (G. Goodman, personal observation).

The direct effect of moult on grooming could be tested by comparing the grooming rates of captive birds with experimentally manipulated moult cycles (cf. Moyer, Gardiner, & Clayton, 2002). Such studies could help determine how much of the seasonal variation in kestrel grooming was caused by moult, versus other factors that may also vary seasonally, such as conspecific signalling (Roulin et al., 2016), coping with stress (Henson et al., 2012) or combatting ectoparasites that may fluctuate seasonally (Foster, 1969; Marshall, 1981). All ectoparasite data in the current study

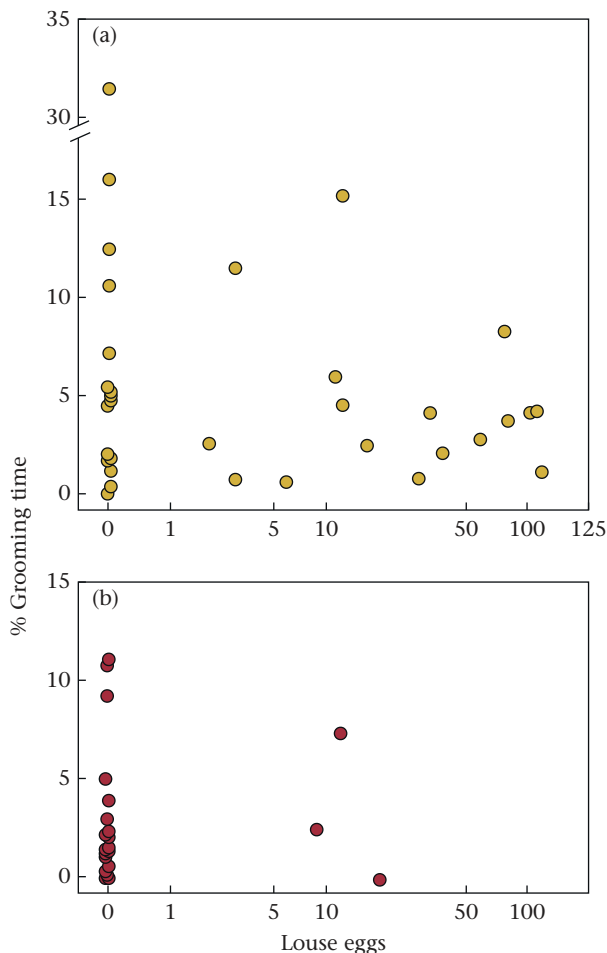


Figure 5. Relationship between grooming and parasite load in (a) Bahama and (b) Utah kestrels in winter. X axes are log scale, with zeros jittered for clarity.

were collected in winter, making it impossible to test for seasonal fluctuations in kestrel parasites. In the future, individual kestrels could be captured every few months to test for seasonal fluctuations in parasite load by tracking the accumulation of eggs on feathers.

Further research on factors that influence seasonal and geographical variation in grooming could shed light on the adaptive consequences of this important behaviour and how it relates to the other adaptive challenges. Although animals presumably experience time–energy trade-offs between grooming and other behaviours, such as foraging, this hypothesis has not been tested rigorously, to our knowledge. If such trade-offs exist, then geographical variation in grooming time may influence other behaviours. For example, birds that groom less in regions with fewer parasites may have more time for foraging and other activities.

In conclusion, avian grooming has a variety of functions, ranging from maintenance of plumage structure to control of ectoparasites, alleviating stress and communicating with conspecifics (Clayton et al., 2010; Henson et al., 2012; Roulin et al., 2016; Simmons, 1985). Most of these functions remain poorly understood in birds; our study focused only on the parasite control function. The adaptive function of grooming in many mammals, as well as most arthropods, also remains poorly understood. Additional research on grooming could prove rewarding for investigators willing to explore this interesting, but understudied, component of animal behaviour.

Author Contributions

S.E.B. and **D.H.C.:** Conceptualization, Data collection and Curation, Methodology, Analysis, Visualization, Validation, Writing of original draft and editing, Funding acquisition. **M.M.W.** and **J.M.H.:** Data collection, Analysis, Validation, Writing - Review and editing. **K.S.H., A.R.C.:** Data collection, Writing - Review and editing. **J.L.W.** and **M.D.O.:** Banding of Utah kestrels, Writing - Review and editing.

Data Availability

The raw data for this study are available as Supplementary material.

Declaration of Interest

None.

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Supplementary Material

Supplementary material associated with this article is available, in the online version, at <https://doi.org/10.1016/j.anbehav.2023.04.015>.

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Appendix

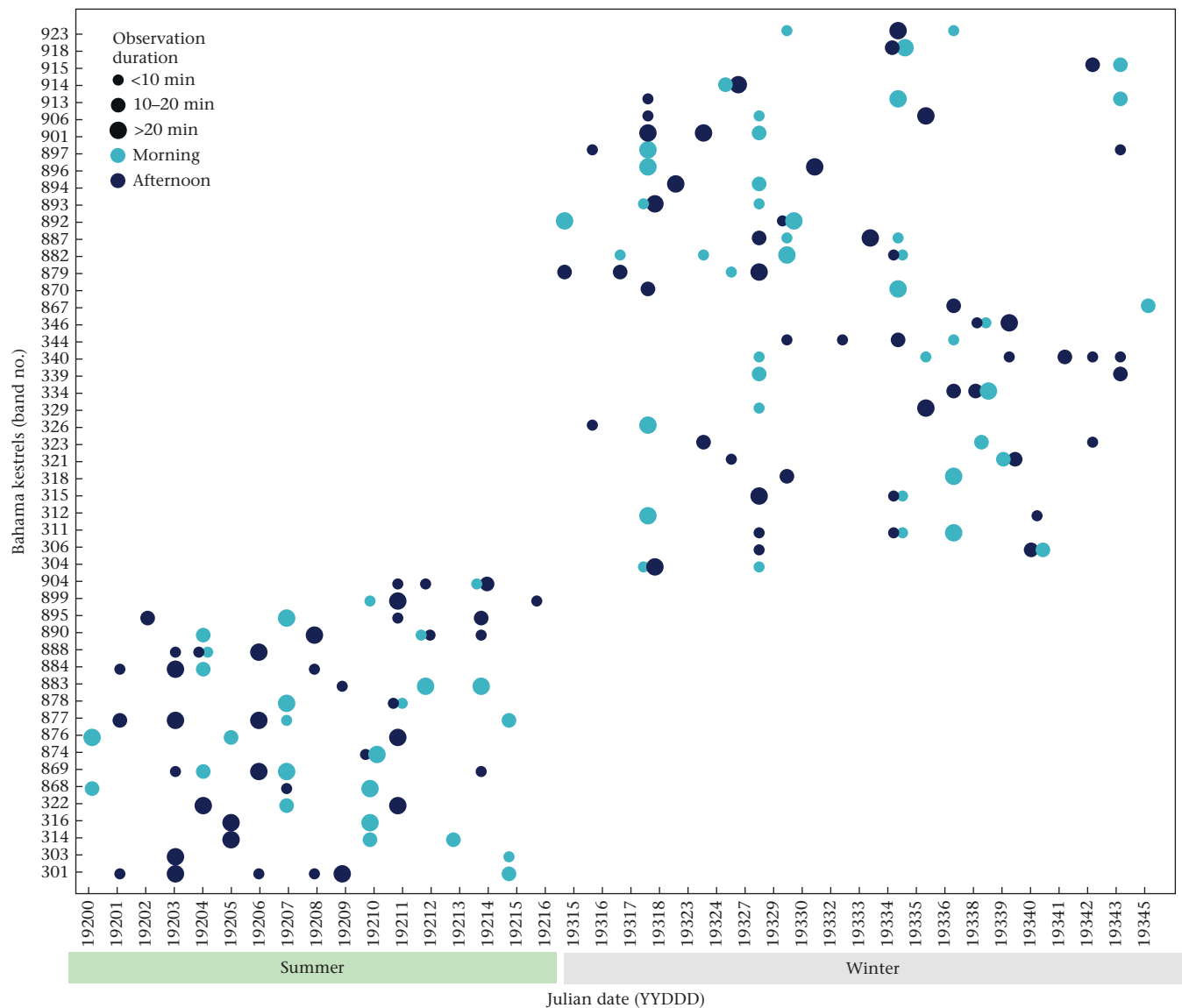


Figure A1. Distribution of behavioural observations of Bahama kestrels over time. Behavioural data for each bird (Y axis) was collected over several observation periods that varied in duration (point size), time of day (point colour), date and season (X axis).

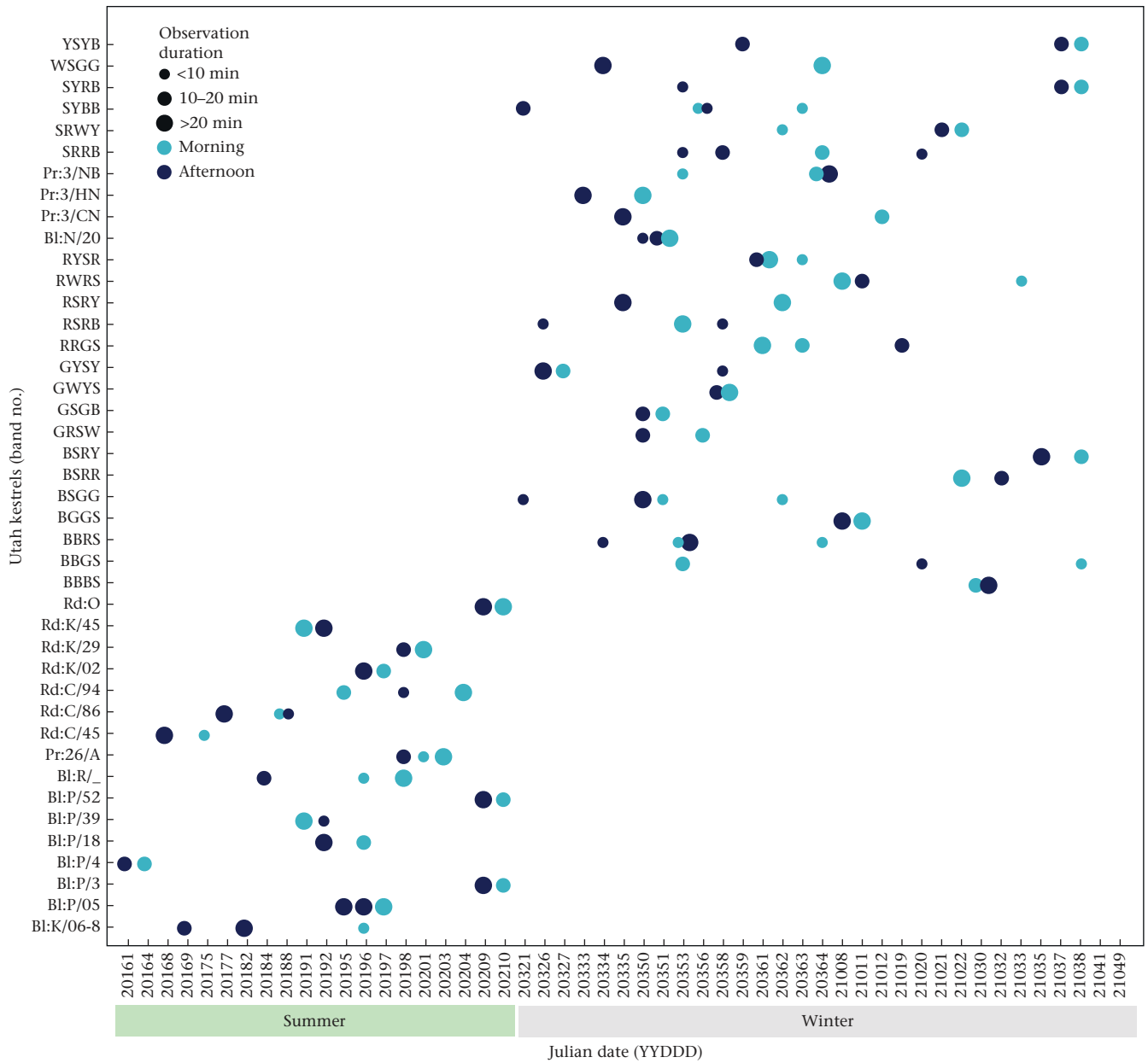


Figure A2. Distribution of behavioural observations of Utah kestrels over time. Conventions as in Fig. A1.