Latitudinal variation in day length and working day length has a confounding effect when comparing nest attentiveness in tropical and temperate species

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Abstract During incubation tropical passerines have been shown to have lower levels of nest attentiveness than their counterparts at north temperate latitudes, spending a higher percentage of daylight time off the nest. This difference has been interpreted as evidence of parental restraint; tropical birds allocate more time to daily self-maintenance, perhaps preserving their higher annual survival rates and future breeding potential. But such comparisons are susceptible to the confounding effects of day length variation, because a given amount of time spent off the nest will account for a greater percentage of daylight time near to the equator than at high latitudes during spring and summer. Based on a pattern of increasing day length between 0° and 70°N we show that the impact of this bias is likely to be small where sites are separated by less than 30–40° of latitude, but should increase substantially both with latitudinal span and distance from the equator. To illustrate this effect we compared nest attentiveness in two congeners, breeding at 1°S and 52°N. During incubation, Stripe-breasted Tits *Parus fasciiventer* in Uganda had a shorter working day (time from emerging to retiring) than north temperate Great Tits *P. major*, and spent a higher percentage of daylight time off the nest (32%) than Great Tits in the UK (24%). However this difference was almost wholly explained by the latitudinal difference in day length; the amount of time spent off the nest differed by just 10 min d^{-1} (<1% of the 24-hr cycle). We show that this effect may be moderated by the change in working day length, which increased less rapidly (in relation to latitude) than day length. Although these effects can thus confound latitudinal comparisons of nest attentiveness, accentuating a pattern predicted by life history theory, they are avoidable if attentiveness is expressed simply as the percentage of time or the number of minutes spent incubating per 24 hours.

Keywords Nest attentiveness; Latitudinal variation; Day length; Working day; Stripe-breasted Tit *Parus fasciiventer*; Great Tit *Parus major*

Introduction

Life history theory would predict that long-lived, tropical species should exercise greater parental restraint than their short-lived, temperate counterparts (Moreau 1944, Williams 1966, Martin 2002). Several studies have thus demonstrated that tropical songbirds spend a lower percentage of daylight time incubating (i.e. show lower nest attentiveness or attendance) than ecologically similar species at higher latitudes (e.g. Martin 2002, Chalfoun & Martin 2007, Cox & Martin 2009). This pattern may reflect regional differences in the time required to obtain sufficient food, or might enable tropical species to reduce the daily energy cost of incubation, instead allocating a higher proportion of the day to self-maintenance. Although low attentiveness is likely to extend the incubation period (Lyon & Montgomerie 1985, Conway & Martin 2000; but see Tieleman et al. 2004), any increased risk to the clutch might be outweighed if the parent's survival and future breeding potential are thereby enhanced (Martin 2002).

The percentage of daylight time spent incubating has been used widely as a measure of nest attentiveness (e.g. Howell & Dawson 1954, Martin & Ghalambor 1999, Martin 2002, Pearse et al. 2004, Fontaine & Martin 2006, Martin et al. 2006, Auer et al. 2007a,b, Chalfoun & Martin 2007, Fierro-Calderón & Martin (2007), Martin et al. 2007, Cox & Martin 2009, Kirkham & Davis 2013). Typically, the amount of time adults spend on- and off the nest is videoed or observed directly for short periods during daylight hours, or else recorded throughout the 24-hr period using thermal sensors. Time spent on the nest has been shown to vary in relation to adult survival (Martin 2002), food availability (Pearse et al. 2004, Chalfoun & Martin 2007, Londoňo et al. 2008), predation levels (Conway & Martin 2000, Fontaine & Martin 2006, Rompré & Robinson 2008), temperature (Conway & Martin 2000, Londoňo et al. 2008, Camfield & Martin 2009) and allo-feeding rate (Pearse et al. 2004, Lloyd et al. 2009), as well as latitudinal zone.

Theoretically, however, observations made during daylight hours could be susceptible to the confounding effects of day length variation when regional comparisons are made, since low attentiveness during short equatorial days may be offset by the additional time spent incubating over correspondingly longer nights (Ricklefs & Brawn 2013). Moreover, a given amount of time spent off the nest is likely to account for a higher percentage of daylight time at the equator than at high latitudes, during spring and summer. Thus, if two diurnal species breeding at locations with 12 and 18 hours of daylight each spend four hours off the nest daily, this will account for 33% and 22% of the daylight time available to them, respectively. Nest attentiveness would therefore appear to be lower in the first species (67% of daylight time spent incubating) than the second (78%), even though both species allocate the same amount of time to daily self-maintenance.

Variation in the length of the 'working day' will also influence patterns of nest attentiveness, introducing a further potential bias. Although an incubating Arctic species may have 24 hours in which to forage off the nest, it may choose to do so for only a limited period: its effective 'working day' (the period between first leaving and last returning to the nest for a prolonged, continuous, 'overnight' period, e.g. Cresswell et al. 2004). For example, in north temperate tit (*Parus*) and flycatcher (*Ficedula*) species the length of the working day increases with latitude, such that parents in southern Europe and Japan have a shorter working day than those in central and northern Europe (Kluijver 1950, Eguchi 1980, Mace 1989, Sanz 1999). But at extreme northern latitudes parent birds may be constrained from exploiting fully the extra daylight time available, and instead incubate more continuously when the sun is low, coinciding with lower temperatures (Tulp & Schekkerman 2006, Tombre et al. 2012) and increased predator activity (Tombre et al. 2012). In addition, parents may simply be physiologically incapable of remaining active throughout the daylight period (Sanz et al. 2000). As a result, day length variation could have a further, non-linear effect on nest attentiveness, if it is moderated by variation in working day length.

Potential effects of variation in day length and working day length on the measurement of nest attentiveness are illustrated in Fig. 1. In each hypothetical example we have assumed that the number and duration of periods spent off the nest ('off-bouts'), and the period for which the nest is observed, are constant, but that day length and working day length vary in relation to latitude. We would predict that, first, during long days (at high latitudes) fewer off-bouts would be recorded during the fixed observation period, than at lower latitudes (Fig. 1a). Second, for a given day length, fewer off-bouts would be recorded in species with a relatively long working day (Fig. 1b). Third, if working day length, as a proportion of the total day length, decreases with latitude (e.g. Sanz et al. 2000), the number of off-bouts recorded at high-latitude sites will be smaller than would be expected, based on day length alone (Fig. 1c).

Here, we examine the effects of variation in day length and working day length on the measurement of nest attentiveness at a range of latitudes, from 0° to 70°N. We examine their effects both theoretically and empirically, in two congeners: the Great Tit *P. major*, at north temperate latitudes, and the Stripe-breasted Tit *P. fasciiventer,* at 1°S (to cover the full latitudinal range). The extent to which day length differs between two locations, and hence influences the measurement of nest attentiveness at each, will depend on the timing of breeding at each location, the latitudinal distance between them and their distance from the equator. We model this and show that:

1. when controlling for these variables, there is a curvilinear relationship between day length and increasing latitude across study sites for the two tit species;

2. the wider the latitudinal separation between locations, as between Stripe-breasted and Great Tit sites, the greater the apparent disparity in nest attentiveness when a fixed amount of time is spent off the nest; and

3. Stripe-breasted and Great Tit nest attentiveness comparisons will therefore differ much more when comparing attentiveness as a proportion of daylight than as a proportion of the 24-hr period. We then compare day length with working day length to determine whether the relationship between these two variables introduces an additional bias, as predicted. Finally, we create an integrated model demonstrating that variation both in day length and working day length can result in biased estimates of nest attentiveness with latitude.

Methods

Day length in relation to latitude

To determine the pattern of change in day length and working day length in relation to latitude, we collated estimates of these values at different stages of the breeding cycle, from a wide geographical spread of Great Tit study sites, based on published accounts, and from a single Stripe-breasted Tit study site. Where no day length value was provided, we estimated this for the mid-date of the relevant stage of the breeding cycle. The mid-point of the incubation period was derived from the mean or median date of clutch initiation quoted for the study site in question, by adding the mean laying period (9 d; derived from the mean clutch size, assuming one egg laid d^{-1}) and half of the mean incubation period (14 d; Cramp & Perrins 1993). We then estimated day length for this date, derived from the latitude and longitude of the study site, using USNO (2012). Similarly, to estimate day length at the mid-point of the nestling period, we added the mean clutch size, incubation period and half of the nestling period (19 d; Cramp & Perrins 1993) to the date of clutch initiation. Although we used the same estimates for the duration of the laying, incubation and nestling periods for all Great Tit sites (from Cramp & Perrins 1993), regional variation in these three parameters is unlikely to have influenced the mid-date, and hence the estimated day length, substantially.

To examine the relationship between day length and latitude throughout the range 0–70°, we used sunrise and sunset data from USNO (2012) to compile day length values at 2.5° intervals on the Greenwich Meridian for a single date (15 May 2012), coinciding approximately with the incubation period for a high proportion of spring-nesting songbirds at north temperate latitudes. We assumed that a hypothetical species spends 230 min off the nest each day during incubation, this value being close to the amount of time spent off the nest by incubating Stripe-breasted and Great Tits (see below). We calculated the percentage of daylight time that 230 min would represent at each 2.5° interval. Since the relationship between day length and latitude is non-linear, we compared the percentage of daylight time that this would represent at pairs of locations (e.g. 10° apart) at different distances from the equator, up to 70°N. We also progressively increased the latitudinal separation between paired sites, in steps of 10°.

Day length and attentiveness in two congeners

To examine the effects of day length variation on nest attentiveness in two congeners we estimated the amount of time spent incubating by the two *Parus* species at two study sites. Over a 15-yr period we recorded time spent on- and off the nest by female Stripe-breasted Tits breeding in nestboxes in the vicinity of the Institute of Tropical Forest Conservation (ITFC) field station at Ruhija, Bwindi Impenetrable Forest, SW Uganda. At 1°02'S, day length at Ruhija varies by just 9 min throughout the year (based on USNO 2012), and laying has been recorded in 10 calendar months (P.S., unpublished).

Each occupied nestbox was watched for periods of 1–7 hrs from 07:00 to 19:00, during which time the arrivals and departures of each adult were recorded. We assumed that females (who undertake all of the incubation) remained inside the nestbox between sunset (mean: 19:04 hr) and sunrise (06:57 hr; from USNO 2012). Since the period of twilight is

very short at this latitude, darkness lifts and falls very quickly, precluding any significant activity before or after sunrise and sunset, respectively. We calculated the mean percentage of time spent inside the box during each hour of daylight, between 07:00 and 19:00, using data pooled from all nests, over days 4–10 of the incubation period (where day 0 = date of clutch completion). We averaged these hourly mean percentages, and multiplied the result by the mean day length at Ruhija (727 min) to estimate the number of minutes spent on- and off the nest during daylight time.

We compared our estimate with the amount of time female Great Tits spent incubating in nestboxes at Wytham Woods, Oxford, UK (51º46'N). During May 2000 a small flexible temperature probe was placed next to the eggs in a sample of nests, after 2–4 eggs had been laid. The temperature of the eggs was logged every 30 s using Tinytag Dataloggers (Gemini Dataloggers Ltd). The temperature trace from each nest was used to determine the start and end of each incubation bout during days 4–10 of the incubation period (for details, see Cresswell & McCleery 2003). For each nest, the total amount of time spent incubating in each 24-hrs was expressed as a percentage of day length (sunrise–sunset; from USNO 2012) for the dates in question.

Day length and working day length

We compared working day length with day length from six Great Tit study sites and one Stripe-breasted Tit study site, to determine whether they showed a linear or curvilinear relationship (see Fig. 3 for sources). Estimates were drawn from the nestling period, since fewer published data were available for the incubation period. The relationship between day length and working day length was examined in the two species by comparing a linear and a quadratic regression model, using AIC. All statistical tests were made using PASW®

STATISTICS 19 software (SPSS Inc., Chicago, IL, USA) and all probabilities are quoted as two-tailed.

Results

Day length variation in relation to latitude

Day length during the nestling period showed a pronounced curvilinear relationship with latitude in the two congeners (Fig. 2a). Our model indicated that a fixed, typical amount of time spent off the nest on a specified date would account for 22.3% of daylight time at 60°N and 31.6% of daylight time at 0°. An equatorial species would therefore appear to show lower nest attentiveness than its north temperate counterpart, the two differing by 9.3 percentage points. Because of the curvilinear relationship between day length and latitude, a given degree of latitudinal separation would be expected to result in a greater disparity in nest attentiveness at higher- than at lower latitudes. For example, we would expect a disparity of 3.6 percentage points between 0° and 30°, 5.7 percentage points between 30° and 60°, and 10.0 percentage points between 40° and 70° (Fig. 2b).

During days 4–10 of the incubation period Great Tit females (*n* = 7 nests, 7 females, 32 d sampled) spent a daily mean of 223 min (±10.27 min S.E.) off the nest, compared with an estimated 233 min for Stripe-breasted Tit females (*n* = 51 nests, >15 females, 922 hrs). Time spent off the nest thus differed between the two species by just 10 min in each 24-hr period, but accounted for 32.0% of daylight time at Bwindi (mean day length: 12.1 hrs) compared with 24.3% of daylight time at Wytham Woods, UK (mean day length: 15.3 hrs). This difference was almost entirely explained by the difference in day length at the two sites; the percentage of time Stripe-breasted Tit females spent off the nest in each 24-hr period at

Bwindi (16.2%) was very similar to that recorded for Great Tit females at Wytham Woods, UK (15.5%) and at other Great Tit study sites in Europe (14–17% 24 hrs^{-1}; Table 1).

The relationship between day length and working day length

Working day length showed a curvilinear relationship with day length (Fig. 3), a quadratic model providing a better fit to the relationship than a linear one (ΔAIC = 6.6; working day length = 2.345 X day length – (0.051 X day $length^2$) –9.334; $F_{2,4}$ = 49.6, P = 0.0015, adjusted R^2 = 0.94). Working day length as a proportion of day length decreased with increasing latitude, accounting for a higher proportion of daylight time for Stripe-breasted Tits in the tropics and for Great Tits in southern Europe than in northern Europe. This change in working day length thus partly offset the confounding effects of day length variation on the measurement of nest attentiveness (e.g. as in Fig. 1c).

To determine the extent to which changes in working day length might ameliorate the bias caused by latitudinal variation in day length when measuring nest attentiveness, we estimated day length at a range of latitudes, on a fixed date, as in Fig. 2b. We then applied the quadratic model shown in Fig. 3, to estimate the working day length of a tit species at each point of latitude, and calculated the percentage of the working day represented by 230 min spent off the nest. Fig. 4 shows the expected level of nest attentiveness, i.e. the percentage of time spent on the nest, at each point of latitude. We would expect nest attentiveness, as a percentage of day length and of working day length, to show a curvilinear increase with latitude when based on a fixed amount of time spent off the nest daily. The level of increase should be lower if attentiveness is measured as a percentage of the working day rather than as a percentage of total day length; but only if it is measured in the middle of the day. If it is measured from sunrise onwards nest attentiveness should be higher and should increase more steeply as a proportion of working day length than as a

proportion of total day length (Fig. 4). This is because sitting adults would remain on the nest throughout the initial part of the observation period, between sunrise and the start of the working day, raising the overall percentage of time spent on the nest during the observation period. The extent to which this would raise their attentiveness level would depend on the length of the observation period, the effect being greater for a shorter (4-hr) period than a longer (6-hr) period (Fig. 4).

Discussion

The relatively low level of attentiveness evident at nests of tropical and south temperate songbirds has been interpreted as a form of parental restraint; breeding adults reduce the daily energy demands of incubation and allocate more time to self-maintenance, perhaps improving their own long-term survival and future breeding potential (Martin 2002). Nest attentiveness has thus become a significant and revealing trait in life history studies, perhaps aided by the fact that it is relatively easy to measure during daylight hours. However this measure has an inherent bias, since day length is shorter at lower latitudes than at high latitudes in the spring and summer, when most temperate songbirds breed. Furthermore, any difference in diurnal attentiveness may be offset by the amount of time spent on the nest during the night-time period, which is typically longer in the tropics (Ricklefs & Brawn 2013). Thus, regional comparisons based on daylight attentiveness may be confounded by day length differences, accentuating the latitudinal trend predicted by life history theory.

We predicted that the scale of this bias is likely to increase with the latitudinal distance between two study sites, and in relation to their distance from the equator. This was borne out by the pattern of change in day length during the breeding season at *Parus* study sites in Europe, Japan and Uganda. Day length during the nestling stage varied much less between sites at 1° and 33° (differing by *c.* 1.8 hr) than between 33° and 65° (differing by *c.* 8.5 hr)

(Fig. 2a). Any bias caused by variation in day length is therefore less likely to influence comparisons between tropical and sub-tropical sites than between two temperate sites that are the same latitudinal distance apart.

A similar, but less pronounced pattern was evident in our model, based on a hypothetical species breeding at latitudes from 0° to 70°N, on a fixed date. Day length would be expected to differ by 1.7 hrs between 1°N and 33°N, but by 4.9 hrs between 33°N and 65°N. The latter prediction (4.9 hrs) was much lower than the difference evident at Great Tit study sites at these latitudes (8.5 hrs; Fig. 2a), based on their laying dates. This was because Great Tits breeding at lower latitudes in Europe and Japan tend to lay in mid- to late April, while those laying at 65° N (in Finland) did so in the second half of May (Orell & Ojanen 1983), by which time day length has increased substantially.

At high latitudes adults may be constrained from utlising all of the daylight time available to them, due either to diurnal variation in temperature or predation pressure (Tulp & Schekkerman 2006, Tombre et al. 2012) or to physiological limitations (Sanz et al. 2000, Cresswell et al. 2004). Sanz et al. (1998, 2000), for example, have shown that Great Tits breeding at 65°N had a working day length of 17.6 hrs; just 78% of the daylight time available (22.5 hrs). In this study the day length and working day length recorded at *Parus* study sites, including that described by Sanz et al. (1998, 2000), showed a positive, curvilinear relationship, such that Great Tits with 22.5 hrs of daylight available would be expected to have a working day of 18.2 hrs, or 81% of the daylight period. Thus, adults at high latitudes are likely to spread the time that they spend off the nest over a shorter period (the working day) than would be expected for their latitude. Our model (Fig. 4) shows that this should ameliorate the impact of the day length bias described here, but only if attentiveness is measured in the middle of the day. If instead the observation period begins at sunrise, as is often the case (e.g. Martin & Ghalambor 1999, Auer et al. 2007a,b, Martin

2002, Chalfoun & Martin 2007, Cox & Martin 2009) and is relatively short (4–6 hrs), nest attentiveness would be expected to show a *greater* increase with latitude than would be predicted from the change in day length alone. In summary, the latitudinal bias is likely to be less pronounced than expected in species with a relatively short working day, if the observation period spans the middle of the day, but *more* pronounced if the observation period begins or ends at sunrise or sunset.

Importantly, our findings indicate that any bias caused by differences in day length between two sites is likely to be small, unless one or both sites lie above 30–40°, and they are widely separated latitudinally. In studies where nest attentiveness has been compared between sites their latitudinal separation has often been small, and the sites in question have been at low latitudes. Martin (2002), for example, compared nest attentiveness at sites in the southern USA, Argentina and South Africa, with an absolute latitudinal separation of just 7–8°. Furthermore, he and co-workers have demonstrated marked differences both in nest attentiveness, the duration of on- and off-bouts during incubation, and in the level of attentiveness evident in north- and south temperate species at similar (absolute) latitudes (Martin 2002, Chalfoun & Martin 2007).

In several studies, however, nest attentiveness has been compared over a wide latitudinal span, encompassing sites at which day-length differences are likely to have been substantial. Chalfoun & Martin (2007) and Cox & Martin (2009) each compared attentiveness between groups of tropical and temperate species, the latter drawn mainly from North America, and including sites at up to 65°N (Chalfoun & Martin 2007) and 47°N (Cox & Martin 2009). In each case the mean attentiveness rate for north temperate species exceeded that of their tropical counterparts, by *c.* 9 percentage points (11 families) and 13 percentage points (Parulids), respectively. These differences were only slightly higher than that described here for Stripe-breasted and Great Tits (8 percentage points) which, as we have

shown, was almost entirely explained by the latitudinal difference in day length. Our findings suggest that comparisons across such widely separated sites are thus likely to have been confounded to some degree by day-length effects, and by the interaction between day length and working day length.

In conclusion, although variation in day length and working day length can confound latitudinal comparisons of nest attentiveness, these effects are avoidable if attentiveness is expressed simply as the percentage of time, or the number of minutes, spent incubating in each 24 hours, rather than as a percentage of daylight time. This is achievable if observations are made (e.g. using thermal sensors) throughout the 24-hr period or the entire daylight period, or if estimates based on shorter observation periods are adjusted to take account of day length and working day length at the sites in question.

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Table 1 Time spent off the nest by Stripe-breasted Tit and Great Tit females during incubation, expressed as a percentage of daylight time, and as a percentage of each 24-hr period.

Species	Location	Stage (d)[1]	Time off nest (min)[2]	% of daylight time	% of 24-hrs	Sources
Stripe-breasted Tit	Uganda	4–10	233	32.0%	16.2%	1
Great Tit	UK	4–10	223	24.3%	15.5%	1
	UK	5–10	197	-	13.7%	2
	The Netherlands	9–10	242	26.4%	16.8%	3
	Czech Republic	1–8	-	25.0%	-	4

[1] Where day 0 = clutch completion.

[2] In each 24-hr period

Sources: 1: This study; 2: Bryan & Bryant (1999); 3: from de Heij et al. (2008); 4: Matysioková & Remeš (2010).

Figure legends

Fig. 1. Diagram to illustrate how an observation period of less than 24 hours duration might give a biased measure of time off the nest, due to: **a.** variation in day length with latitude; **b.** variation in working day length; **c.** the interaction between the two, where working day length varies as a proportion of day length. In each 24-hour period incubating parents have 16 periods of the same duration off the nest ('off-bouts':) between sunrise ( ) and sunset ( ). Each nest is observed for 4 hours. The number of off-bouts recorded (shown at right) will vary with day length and working day length, such that nest attentiveness will appear to vary with latitude, even when time spent off the nest per 24 hours does not.

Fig. 2. **a.** Variation in day length (sunrise–sunset) at *Parus* study sites in Europe, Japan and Uganda during the nestling period, in relation to absolute latitude. ● Great Tit; ■ Stripe-breasted Tit. Sources: Kluijver 1951, Zink 1959, Busse & Gotzman 1962, Lack 1966, Likhachev 1967, von Haartman 1969, Balat 1970, Frederiksen et al. 1972, van Balen 1973, Dunn 1976, Slagsvold 1976, Eguchi 1980, van Noordwijk et al. 1981, Dhondt, A. *in* Orell & Ojanen 1983, Orell & Ojanen 1983, Tinbergen & Dietz 1994, Verhulst & Tinbergen 1997, Sanz et al. 1998, 2000, Wilkin et al. 2009. **b.** The extent to which a given amount of time spent off the nest, expressed as a percentage of daylight time on a specific date, would differ between pairs of sites, in relation to their latitudinal separation and distance from the equator. For example, nest attentiveness would be expected to differ by 3.6 percentage points between sites at 0° and 30°N, but by 10.0 percentage points between 40° and 70°N.

Fig. 3. Working day length (time from emerging to retiring), in relation to day length in *Parus* studies. The dashed line is Y=X, i.e. if working day length exactly reflected available daylight. A quadratic model ($Y = 2.34(X) - 0.05(X^2) - 9.334$) (solid line) indicates that working day length increases less steeply than day length, particularly at high latitudes. ●

Great Tit; ■ Stripe-breasted Tit. Sources: Eguchi 1980, Tinbergen & Dietz 1994, Verhulst & Tinbergen 1997, Sanz et al. 1998, 2000, Wilkin et al. 2009.

Fig. 4. The predicted increase in nest attentiveness with latitude, as a consequence of variation in day length, working day length and their interaction. We assumed that a fixed amount of time is spent off the nest daily; that day length is calculated for a single date and on the Greenwich meridian; and that working day length is derived from day length, using the quadratic model in Fig. 3. Solid line: attentiveness based on day length. Dashed lines: attentiveness based on working day length. **a.** 4-hr observation period at midday. **b.** 6-hr period, commencing at sunrise. **c.** 4-hr period, commencing at sunrise.

Fig. 1

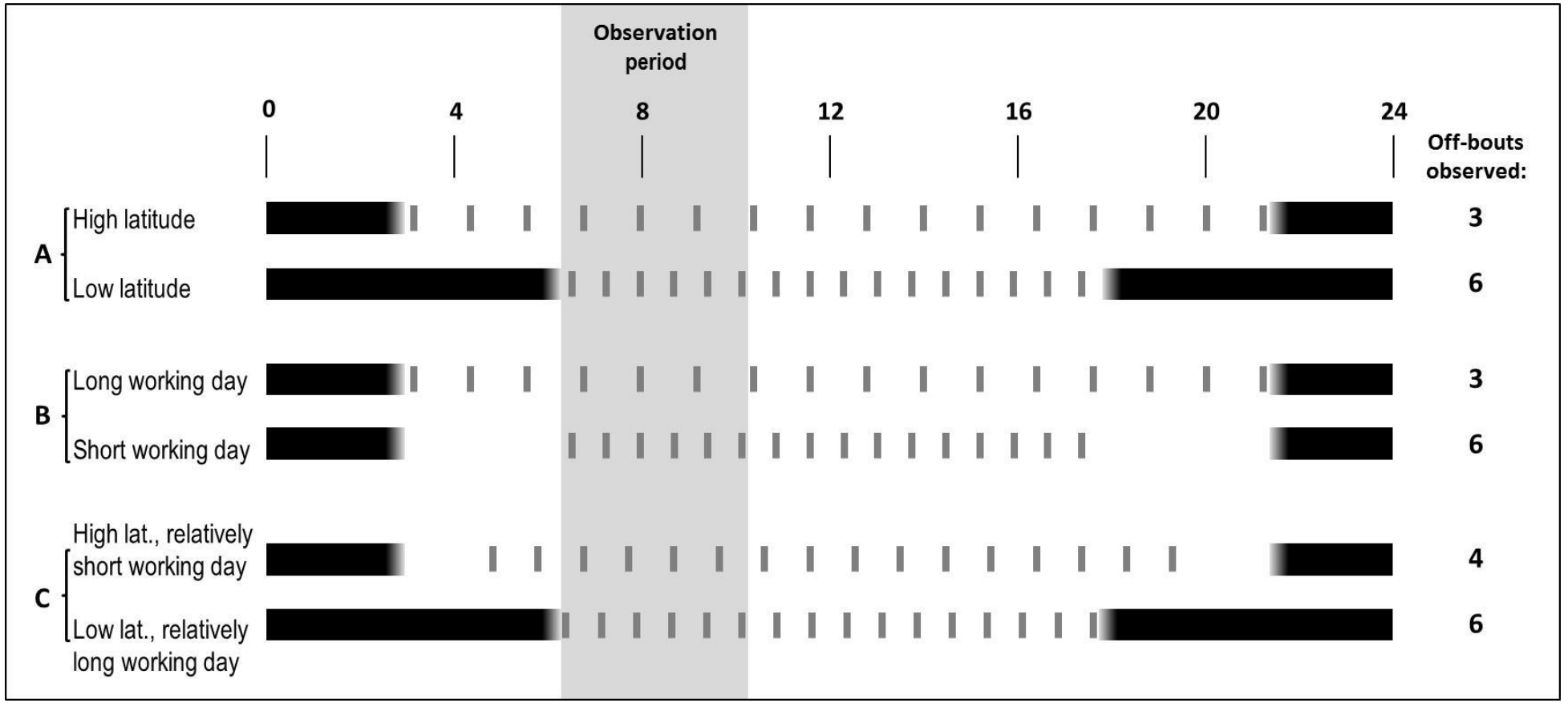
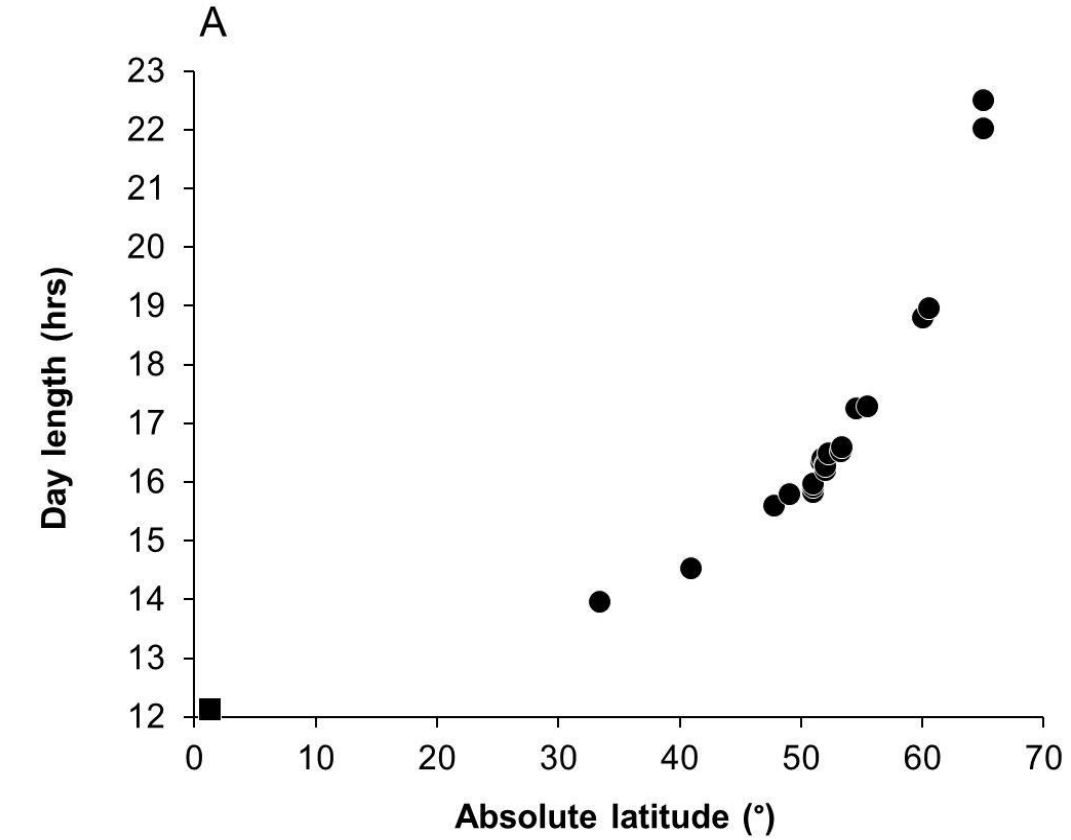

Observation period
0
4
8
12
16
20
24
Off-bouts observed:
A
High latitude
3
Low latitude
6
B
Long working day
3
Short working day
6
C
High lat., relatively short working day
4
Low lat., relatively long working day
6

Fig 2


A
Day length (hrs)
23
22
21
20
19
18
17
16
15
14
13
12
0
10
20
30
40
50
60
70
Absolute latitude (°)

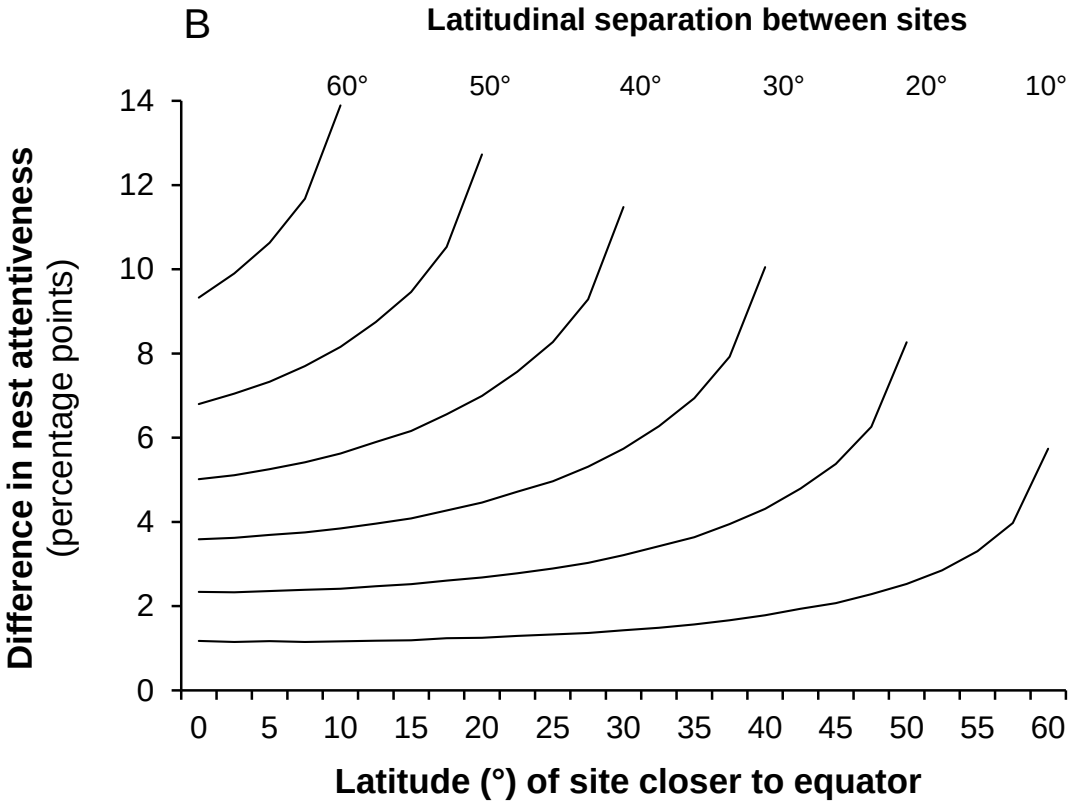

B
Latitudinal separation between sites
60°
50°
40°
30°
20°
10°
Difference in nest attentiveness
(percentage points)
14
12
10
8
6
4
2
0
0
5
10
15
20
25
30
35
40
45
50
55
60
Latitude (°) of site closer to equator

Fig 3.

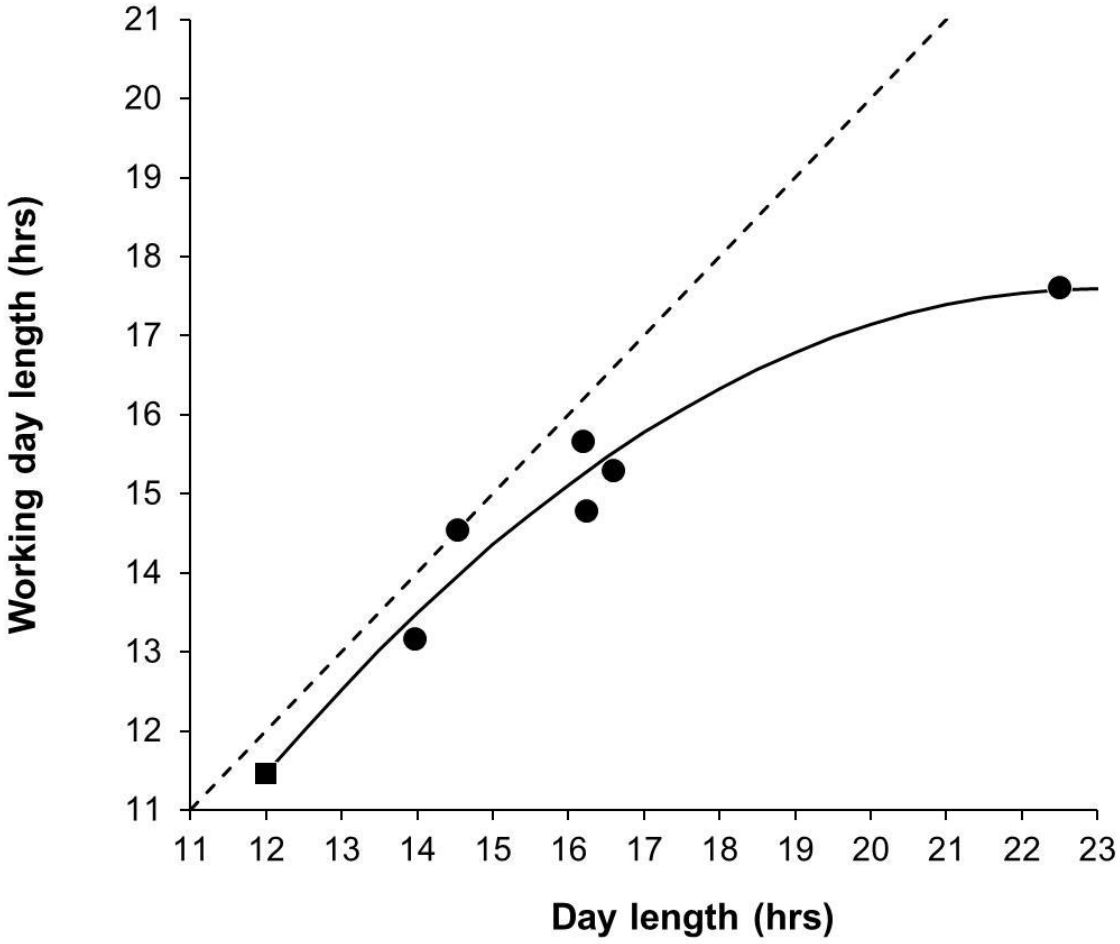
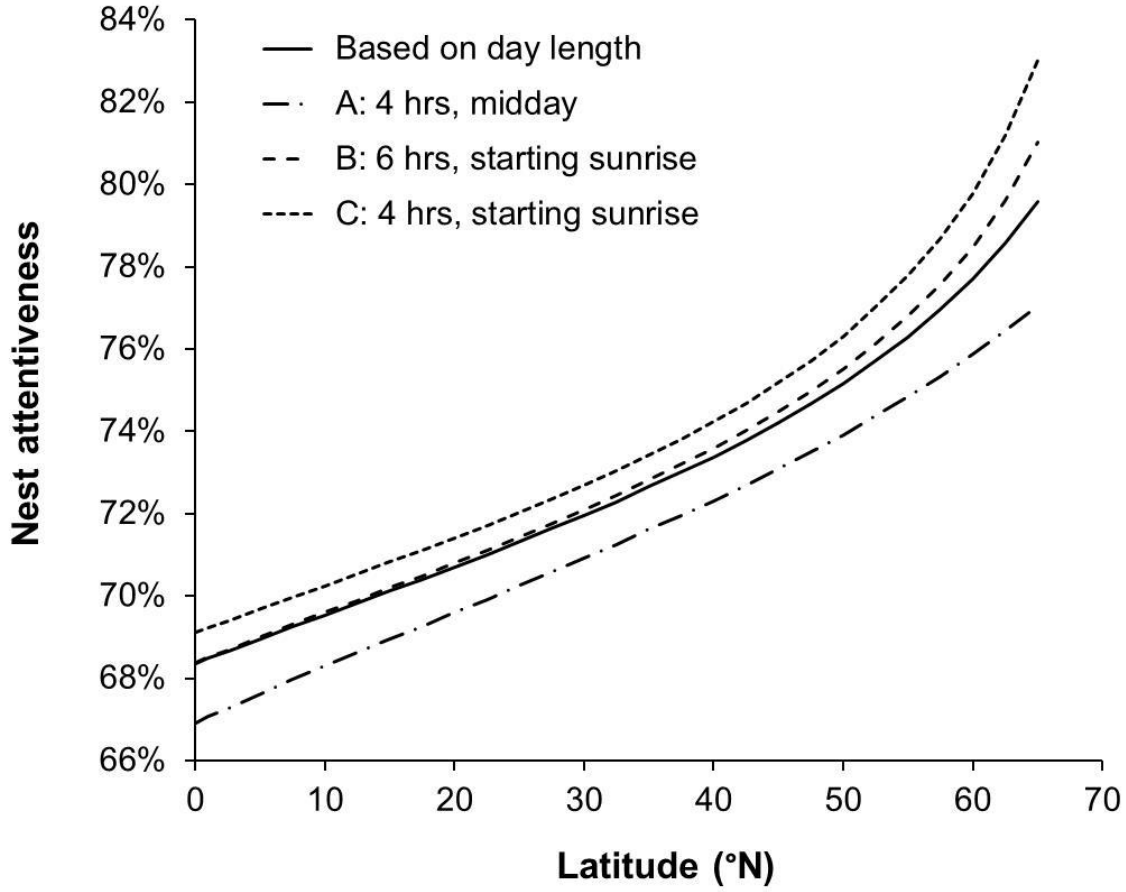

Working day length (hrs)
21
20
19
18
17
16
15
14
13
12
11
11 12 13 14 15 16 17 18 19 20 21 22 23
Day length (hrs)

Fig. 4


84%
82%
80%
78%
76%
74%
72%
70%
68%
66%
Nest attentiveness
Based on day length
A: 4 hrs, midday
B: 6 hrs, starting sunrise
C: 4 hrs, starting sunrise
0
10
20
30
40
50
60
70
Latitude (°N)