

1 **The relationship between behavior, physiology, and a color dimorphism during**
2 **the polar day in a seabird**

3
4 Nicholas Per Huffeldt^{a, b, c, *}, Anna Tigano^{d, e}, Kjell Einar Erikstad^{f, g}, Wolfgang
5 Goymann^h, Susanne Jenni-Eiermannⁱ, Truls Moum^j, Tone Kristin Reiertsen^f

6
7 Please note that surnames are underlined above

8 ^a Greenland Institute of Natural Resources, 3900 Nuuk, Greenland

9 ^b Arctic Ecosystem Ecology, Department of Bioscience, Aarhus University, 4000 Roskilde,
10 Denmark

11 ^c Department of Biology, Wake Forest University, Winston-Salem, NC 27109, USA

12 ^d Department of Molecular, Cellular and Biomedical Sciences, University of New Hampshire,
13 Durham, NH 03824, USA

14 ^e Hubbard Center for Genome Studies, University of New Hampshire, Durham, NH 03824, USA

15 ^f Norwegian Institute for Nature Research, Fram Centre, 9296 Tromsø, Norway

16 ^g Centre for Biodiversity Dynamics, Department of Biology, Norwegian University of Science and
17 Technology, 7491 Trondheim, Norway

18 ^h Abteilung für Verhaltensneurobiologie, Max-Planck-Institut für Ornithologie, 82319 Seewiesen,
19 Germany

20 ⁱ Swiss Ornithological Institute, 6204 Sempach, Switzerland

21 ^j Genomics Division, Faculty of Bioscience and Aquaculture, Nord University, 8049 Bodø,
22 Norway

23 * Corresponding author: Huffeldt, N.P.; nph@bios.au.dk; Twitter: [@nphuffeldt](https://twitter.com/nphuffeldt)

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26 **3-5 Highlights (each bullet 85 characters w/ spaces)**

- 27 • Keeping time in the continuous light of polar day may be challenging
- 28 • Melatonin and corticosterone were measured in a seabird during the Arctic
29 summer
- 30 • Melatonin, but not breeding-site attendance, tracked the diel cycle in common
31 murre
- 32 • Melatonin depended on behavioral state and differed between color morphs
- 33 • Limited variation in the murre's corticosterone profile matched other polar
34 species

35
36 **Abstract (max 250 words, currently 250)**

37 The predictable oscillation between the light of day and the dark of night across the diel
38 cycle is a powerful selective force that has resulted in anticipatory mechanisms in nearly
39 all taxa. At polar latitude, however, this oscillation becomes highly attenuated during the
40 continuous light of polar day during summer. A general understanding of how animals
41 keep time under these conditions is poorly understood. We tested the hypothesis that
42 the common murre (a seabird, *Uria aalge*) can use melatonin and corticosterone,
43 hormones associated with timekeeping, to track the diel cycle despite continuous light.
44 We also tested the assumption that common murre breeding during polar summer
45 schedule their colony attendance by time of day and sex, as they do at subpolar
46 latitude. In the Atlantic population where this study was conducted, common murre
47 have a plumage color dimorphism associated with fitness-related traits, and we

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48 investigated the relationship of this dimorphism with colony attendance, melatonin, and
49 corticosterone. The murre did not schedule their attendance behavior by time of day or
50 sex, yet they had higher concentrations of melatonin and, to a more limited extent,
51 corticosterone during “night” than “day”. The two morphs had different colony-
52 attendance behavior and melatonin concentrations, lending support for balancing
53 selection maintaining the plumage color dimorphism. In common murre, melatonin can
54 signal time of day despite continuous light, and the limited variation of corticosterone
55 across the diel cycle contributes to the mounting evidence that polar-adapted birds and
56 mammals require little or no diel variation in glucocorticoids during polar day.

57

58 Keywords (max 10): Arctic; circadian rhythm; color polymorphism; continuous light;
59 corticosterone profile; daily rhythm; glucocorticoid profile; melatonin profile; midnight
60 sun; *Uria aalge*

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61 **Introduction**

62 The cycling between the dark of night and the light of day regulates many ecological
63 interactions and is a major selective force for optimizing behavior and physiology
64 (Kronfeld-Schor and Dayan, 2003; Pittendrigh, 1993; Schwartz and Daan, 2017). This
65 selection has resulted in anticipatory mechanisms in most organisms in the form of
66 biological rhythms, such as circadian rhythms (Pittendrigh, 1993; Schwartz and Daan,
67 2017). Above the polar circles, however, the 24-h light-dark cycle is greatly attenuated
68 during summer and winter, and investigating the behavior and physiology of polar
69 residents during these seasons is paramount for understanding which mechanisms are
70 the most important for tracking the diel cycle in the wild.

71 Melatonin and glucocorticoids are broadly recognized as endogenous elements
72 of the circadian system because they provide physiological signals of biological rhythms
73 that track daily environmental cycles. Though exceptions exist (e.g., (Ashley et al.,
74 2013; Huffeldt et al., 2020; Jessop et al., 2002), melatonin generally tracks the light-dark
75 cycle by elevating during darkness and falling with increasing light intensity (Gwinner et
76 al., 1997; Pandi-Perumal et al., 2006). In addition to its circadian functions, melatonin
77 serves many other roles, including modulation of the immune system and protection of
78 cellular functions (Pandi-Perumal et al., 2006). Diel patterns of glucocorticoids track
79 circadian rhythms and food intake (Dickmeis, 2009; Kalsbeek et al., 2012; Quillfeldt et
80 al., 2007; Son et al., 2011; Woodley et al., 2003) and commonly link to activity (Jessop
81 et al., 2002; Landys et al., 2006). Glucocorticoids also provide important
82 immunomodulatory and energetic functions, among others (Landys et al., 2006;

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83 Sapolsky et al., 2000). In birds, the primary glucocorticoid is corticosterone. The diel
84 pattern of corticosterone in birds is low during the active phase and high during the
85 inactive phase (Breuner et al., 1999; Landys et al., 2006; Romero and Ramage-Healey,
86 2000; Tarlow et al., 2003). Thus, melatonin and corticosterone can act as redundant
87 physiological signals that entrain internal rhythms to environmental rhythms, which, in
88 the example of a diurnal bird, may ultimately be dictated by obtaining food during the
89 day and conserving energy and avoiding predators at night.

90 During the extreme photic conditions in polar summer and winter, light intensity
91 still cycles in the general environment, with the highest intensities during “daytime”
92 (Ashley et al., 2013; Huffeldt et al., 2020). Melatonin can either track this diel change in
93 light intensity (birds: (Ashley et al., 2013; Cockrem, 1991; Hau et al., 2002; Huffeldt et
94 al., 2020; Silverin et al., 2009); mammals: (Griffiths et al., 1986; Stokkan and Reiter,
95 1994)) or be arrhythmic (birds: (Cockrem, 1991; Miché et al., 1991; Reierth et al., 1999;
96 Steiger et al., 2013); mammals: (Eloranta et al., 1992)). Although glucocorticoids are
97 known to be under the control of the circadian system in mammals (Dickmeis, 2009;
98 Kalsbeek et al., 2012; Son et al., 2011), most studies of glucocorticoids during polar
99 summer describe little to no variation across the diel cycle (birds: (Huffeldt et al., 2020;
100 Steenweg et al., 2015; Vleck and van Hook, 2002) [*cf.* (Scheiber et al., 2017)];
101 mammals: (Barrell and Montgomery, 1989)). To gain better insight into the functional
102 role of melatonin and corticosterone during the continuous light of polar summer, we
103 studied these hormones in a seabird, the common murre (*Uria aalge*).

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104 The common murre is a colonial charadriiform whose range extends from
105 approximately 37 °N to well above the northern polar circle (Gaston and Jones, 1998).
106 In common murre, ecological interactions and colony attendance can depend on time
107 of day. Colony attendance by common murre generally follows a diel pattern
108 (Birkhead, 1978; Thayer et al., 1999; Zador and Piatt, 1999), with most foraging
109 occurring outside of nighttime (Regular et al., 2010). Females are more likely to
110 incubate their egg overnight and males are more likely to incubate their egg during
111 midday (Wanless and Harris, 1986), while the amount of time spent attending the
112 colony not incubating or brooding depends on foraging conditions (Zador and Piatt,
113 1999). Males and females provision their chick diurnally at subpolar latitude, with males
114 spending more time away from the chick during night hours (Thaxter et al., 2009), and
115 murre will also forage with a crepuscular pattern at some colonies (Regular et al.,
116 2010). Above the polar circle at Hornøya (Norway), the same colony where our study
117 was conducted, diel provisioning of the chick is specific to certain times of day in each
118 sex (Holmøy, 2019). Thick-billed murre (*U. lomvia*), a sister species to common
119 murre, maintain robust and sex-stereotyped rhythms of incubating and brooding under
120 both subpolar and polar conditions (Elliott et al., 2010; Huffeldt and Merkel, 2016;
121 Paredes et al., 2006). All this considered, we expect that common murre keep time
122 during the polar summer to schedule their behavior and physiology according to the diel
123 cycle.

124 Despite the several sex-stereotyped behaviors described in common and thick-
125 billed murre, lack of information on colony attendance of the sexes during polar day for

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126 common murre required us to first test the assumption that they have a sex-
127 stereotyped, diel pattern in their incubating and brooding behavior during polar summer.
128 We predicted that males attending the colony would be incubating their egg or brooding
129 their chick (“on-duty”) during “daytime” and females attending the colony would be on-
130 duty during “nighttime” (Thaxter et al., 2009; Wanless and Harris, 1986).

131 We then hypothesized that melatonin and corticosterone provide physiological
132 signals of time of day despite continuous light. Our hypothesis is based on the
133 observations that in common murre sex-stereotyped foraging and chick-provisioning
134 depends on time of day (Thaxter et al., 2009), that their colony is subjected to diel
135 changes in ambient light intensity (e.g., (Huffeldt et al., 2020)), and that melatonin rises
136 in response to slight changes in light intensity in other bird species (Kumar et al., 2000).
137 We predicted that circulating melatonin will be elevated in birds attending the colony
138 during “night” hours compared to “day” hours (e.g., (Ashley et al., 2013; Hau et al.,
139 2002; Silverin et al., 2009)) and that corticosterone will have a typical diel pattern for a
140 diurnal bird, with the lowest concentration during daytime (Scheiber et al., 2017). The
141 alternative hypotheses were that in common murre the continuous light abolishes,
142 directly or indirectly, any diel variation in melatonin, corticosterone, or both.

143 Furthermore, in the Atlantic Ocean, the common murre displays a plumage color
144 dimorphism, with a bridled morph having a white ring around the eye that extends down
145 the auricular groove and an unbridled morph with a completely dark chocolate-brown
146 head. The frequency of the dimorphism and survival of the two morphs are correlated
147 with sea surface temperature, indicating that bridled and unbridled birds have different

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148 thermal adaptations (Birkhead, 1984; Reiertsen et al., 2012). The dimorphism is
149 associated also with differences in parental investment, with mixed-morph pairs raising
150 heavier chicks compared to single-morph pairs (Kristensen et al., 2014), and morph is
151 linked to genes involved in metabolism and circadian rhythms (Tigano et al., 2018).
152 Given that the plumage color dimorphism in common murre is associated with these
153 different traits, we also tested whether morph could predict colony attendance and
154 concentrations of melatonin and corticosterone.

155

156 **Material and methods**

157 *Sample collection*

158 Blood was drawn from 100 common murre (N = 55 females, 45 males) breeding on
159 Hornøya, Norway (70.39 °N, 31.15 °E). Sampling occurred during one breeding season
160 from the 13th to the 26th of June and from the 1st to the 10th of July 2014 under the
161 continuous light of polar summer; during this period the sun never went below the
162 horizon (range of sun angle = 2.66° to 43.05° [obtained from:
163 https://www.sunearthtools.com/dp/tools/pos_sun.php?lang=en and accessed on: 03
164 March 2020]). Time of day is reported in local time: Central European Summer Time
165 (CEST, UTC +2).

166 The murre sampled were recorded as “on-duty” if incubating their egg or
167 brooding their chick, or as “off-duty” if attending their mate that was on-duty (Huffeldt
168 and Merkel, 2016). Generally, two murre, one on-duty and one off-duty, were sampled
169 per sampling event, but in three cases three murre were sampled, and if no off-duty

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170 individuals of known breeding status were present, then on-duty birds were captured.
171 Murres were captured independent of morph using a telescoping noose pole from two
172 plots that were separated visually (approximately 50 m apart). A minimum of 30 min
173 (except once, 22 min) elapsed between captures during the same sampling event. A
174 minimum of 10 h elapsed between sampling events from the same plot. All sampled
175 birds received a metal ring on their tarsus with a unique alphanumeric code, and no
176 birds were sampled twice.

177 Blood was drawn from the brachial vein within 3 min after placing the noose
178 around the bird's head, as capture induces corticosterone to elevate above baseline
179 concentration after approximately 3 min due to corticosterone's role in the physiological
180 response to unexpected noxious stimuli ((Huffeldt et al., 2020; Romero and Reed,
181 2005); Supplementary Corticosterone Analyses)). Blood samples were centrifuged
182 within 4 h of sampling. After centrifugation, the plasma was separated immediately and
183 frozen at -20 °C. The sex of each bird was unknown during sampling, and sex was
184 identified molecularly as in Barrett *et al.* (2015), using DNA extracted from blood and the
185 P2-P8 primer set (Griffiths et al., 1998). All sampling occurred in accordance with the
186 institutional animal care and use committee at Wake Forest University (protocol #: A14-
187 88).

188

189 *Hormone assays*

190 Radio-immunoassay was used to quantify the plasma concentration of melatonin in a
191 single assay following Goymann *et al.* (2008) and Huffeldt *et al.* (2020). The standard

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192 curves and sample concentrations were calculated with *Immunofit 3.0* (Beckman Inc.,
193 Fullerton, CA, USA) using a four-parameter logistic-curve fit. Mean (\pm sd) extraction
194 recovery of melatonin was 77 ± 3.1 %. The intra-assay coefficient of variation for
195 standard melatonin was 3.4 % and for stripped chicken plasma with melatonin was 2.7
196 %, and the detection limit was 4.1 pg/mL. Only samples with a plasma volume $> 30 \mu\text{L}$
197 were assayed and included in our analyses. Corticosterone was prioritized if plasma
198 volume was not sufficient to assay both hormones.

199 Enzyme-immunoassays were used to quantify the plasma concentration of
200 corticosterone following Jenni-Eiermann *et al.* (2015) and Huffeldt *et al.* (2020).
201 Samples were measured in triplicate, and the concentration of corticosterone in plasma
202 samples was calculated using the standard curve run in duplicate in each assay. The
203 inter-assay variation was 15.5 % and the intra-assay variation was 9.8 %. The detection
204 limit was 1.21 ng/mL. Samples that were below the detection limit ($N = 2$) were assigned
205 the value of the detection limit (Barrett *et al.*, 2015).

206

207 *Statistical analyses*

208 The *R* programming environment (v. 3.5.1) was used for all statistical analyses (R Core
209 Team, 2018). An information-theoretic approach (Burnham *et al.*, 2011; Burnham and
210 Anderson, 2004) and the *MuMIn* package in *R* (Barton, 2018) were used to identify the
211 ability of predictor variables to explain variation in our dependent variables and thus to
212 test our hypotheses. A mix of an exploratory and hypothesis testing framework was
213 used to investigate colony attendance, melatonin, and corticosterone. A saturated

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214 model including all the relevant predictors and interactions was fitted to the data, and
215 then all relevant models derived from the saturated model were ranked using Akaike
216 Information Criterion corrected for small sample size (“AICc”) and the “dredge” function
217 (*MuMIn*, (Barton, 2018); Supplementary Model Sets). The models that included only
218 time of day, only morph, and the interaction between sex and time of day (the latter for
219 colony attendance analyses only) were compared to the null model using evidence
220 ratios of the model to the null model, and these ratios were used to test the probability
221 of our hypotheses given our data (Burnham et al., 2011). Figures were produced by
222 calling *ggplot2* (Wickham, 2016) from *visreg* (Breheny and Burchett, 2017).

223 Model fit was checked visually using plots of residuals vs. fitted values and QQ
224 plots of the residuals. The “heatmap.fit” function from the *heatmapFit* package in *R* was
225 used to check model fit of generalized linear models (“GLMs”) with binomial error
226 structures (Esarey et al., 2016). Hour of day was used as the predictor variable for time
227 of day. Because time of day is a circular variable, it was transformed into two linear
228 variables by converting hour of day to radians and including the sine and cosine of the
229 radian as continuous predictor variables (Cox, 2006). The top model, the null model, the
230 relevant models for testing our hypotheses, and the model summaries of top models are
231 reported in the results section. The complete model sets and relevant model summaries
232 can be found in the supplementary material (Supplementary Model Sets;
233 Supplementary Results). Means are reported with the 95% credible interval (mean [95%
234 CI]) unless noted otherwise.

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235 GLMs with a binomial error structure were used to assess which predictor
236 variables had an effect on whether an individual's attendance was either off-duty ("0") or
237 on-duty ("1"). The saturated model included the predictors: sex (categorical: female,
238 male), morph (categorical: bridled, unbridled), time of day (continuous), and day of year
239 (continuous), with three-way interactions among morph, sex, and time of day. Day of
240 year was included as a proxy for changes occurring across the breeding season. To
241 understand better the scheduling of on-duty attendance in common murrelets and to test
242 the hypothesis that the sex of on-duty birds depended on time of day, the sex of on-duty
243 individuals (male = "0", female = "1") was used as the dependent variable in a GLM with
244 a binomial error structure. The saturated model included the predictors: time of day,
245 morph, the interaction of morph with time of day, and day of year.

246 Melatonin concentration was log-transformed prior to modelling to adhere to
247 model assumptions. GLMs with a gamma error structure were used to assess the
248 association of our predictor variables with the dependent variable melatonin. The
249 saturated model included the predictors: attendance (categorical: off-duty, on-duty), sex,
250 morph, nest content (categorical: egg, chick), day of year, and time of day. The
251 saturated model had three-way interactions among sex, attendance, and time of day.

252 Corticosterone concentration was log-transformed prior to modelling to adhere to
253 model assumptions. Linear models ("LMs") were used to assess the association of our
254 predictor variables with the dependent variable corticosterone. The saturated model
255 included the predictors: attendance, sex, morph, nest content, day of year, and time of

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256 day. The saturated model had three-way interactions among sex, attendance, and time
257 of day.

258

259 **Results**

260 *Colony attendance behavior*

261 Information on colony attendance behavior was not available for one individual, which
262 was excluded from further analysis (N = 99). Morph was the best predictor of whether a
263 bird attending the colony was on- or off-duty, and, given our data, the model including
264 only morph was 2.29 times more likely to predict whether a bird attending the colony
265 was on- or off-duty than the null model (Table 1a). Unbridled individuals were on-duty
266 more often than bridled individuals (Fig. 1). The interaction between sex and time of day
267 was 0.03 times as likely as the null model to explain whether a bird at the colony was
268 on- or off-duty given our data (Table 1a), thus indicating that common murres do not
269 have a sex-stereotyped, diel pattern in on- and off-duty attendance during polar day.

270 When only sex of on-duty birds was the dependent variable (N = 67), the null
271 model was the top model (Table 1c, d) and the models including only morph and only
272 time of day were, respectively, 0.35 and 0.17 times as likely as the null model to predict
273 the sex of on-duty birds (Table 1c). Therefore, models including time of day and morph
274 provided an insubstantial ability to predict the sex of on-duty birds, and the sex of on-
275 duty birds depended on neither time of day nor morph.

276

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277 **Table 1. Model results for attendance behavior.** (a) Model selection table including
 278 the top model, models testing our hypotheses, and the null model testing the
 279 association among on- and off-duty attendance, and (b) the model summary of the top
 280 model testing the association among on- and off-duty attendance. (c) Model selection
 281 table including the top model, models testing our hypotheses, and the null model testing
 282 the association of sex of only on-duty birds, and (d) the model summary of the top
 283 model testing the association of sex of only on-duty birds. “ER” is the evidence ratio of
 284 the model to the null model following Burnham *et al.* (2011).

Dependent variable: on- and off-duty attendance

(a) Model selection list

Model parameter(s)	AICc	ΔAICc	ER
morph	124.98	0	2.29
null	126.63	1.65	
cosine(time of day) + sine(time of day)	130.71	5.73	0.13
cosine(time of day)*sex + sine(time of day)*sex	133.55	8.57	0.03

(b) Summary of top model

	Estimate	95% CI	Z	P
intercept	0.22	-0.43 to 0.89	0.67	0.51

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morph: unbridled 0.85 -0.01 to 1.73 1.93 0.05

Dependent variable: sex of on-duty birds only

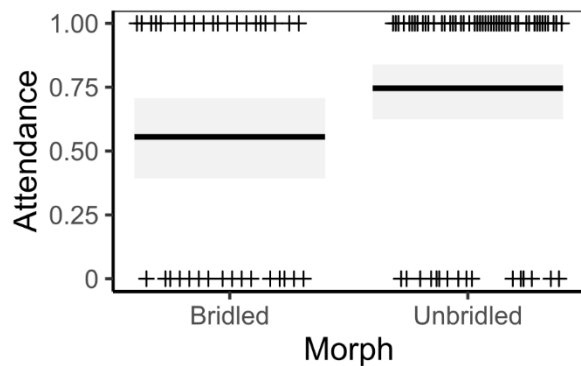
(c) Model selection list

Model parameter(s)	AICc	ΔAICc	ER
null	93.73	0	
morph	95.82	2.09	0.35
cosine(time of day) + sine(time of day)	97.31	3.58	0.17

(d) Summary of top model

	Estimate	95% CI	Z	P
intercept	0.27	-0.21 to 0.76	1.1	0.27

285



286

287 **Figure 1. Colony attendance behavior of the two morphs.** The solid lines and

288 shaded areas are the reverse-transformed predicted values and 95% credible intervals,

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289 respectively, from the top model. “+”s are individual data points (1 = on-duty attendance,
290 0 = off-duty attendance).

291

292 *Melatonin*

293 Eighty-seven individuals had information for all the predictors included in the saturated
294 model. The mean concentration of melatonin was 20.11 [18.32 to 21.90] pg/mL (median
295 = 16.15 pg/mL, range = 13.51 to 58.04 pg/mL). The model including attendance and
296 time of day was the best at predicting melatonin concentration, and, given our data, this
297 model was 42.76 times more likely than the null model to predict melatonin
298 concentration (Table 2a). Individuals that were on-duty had a higher concentration of
299 melatonin than those attending the colony off-duty, and melatonin increased during
300 night and decreased during day in birds attending the colony (Fig. 2). The model
301 including only morph was 1.87 times more likely to predict melatonin concentration than
302 the null model given our data (Table 2a; Supplementary Results), thus, indicating that
303 morph was able to predict melatonin concentration in the common murrelets studied. The
304 higher melatonin concentration in on-duty birds compared to off-duty birds was most
305 pronounced in unbridled murrelets; however, the pattern persisted in both morphs despite
306 the overall lower melatonin concentration in bridled murrelets when the interaction
307 between attendance and morph was accounted for in a separate analysis (Fig. 3;
308 Supplementary Results).

309

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310 **Table 2. Model results for melatonin.** (a) Model selection table including the top
 311 model, models testing our hypotheses, and the null model for predicting melatonin
 312 concentration. (b) The model output summary of the top model. “ER” is the evidence
 313 ratio of the model to the null model following Burnham *et al.* (2011).

Dependent variable: melatonin

(a) Model selection list

Model parameter(s)	AICc	ΔAICc	ER
attendance + cosine(time of day) + sine(time of day)	47.95	0	42.76
cosine(time of day) + sine(time of day)	51.42	3.47	7.53
morph	54.20	6.25	1.87
null	55.46	7.51	

(b) Summary of top model

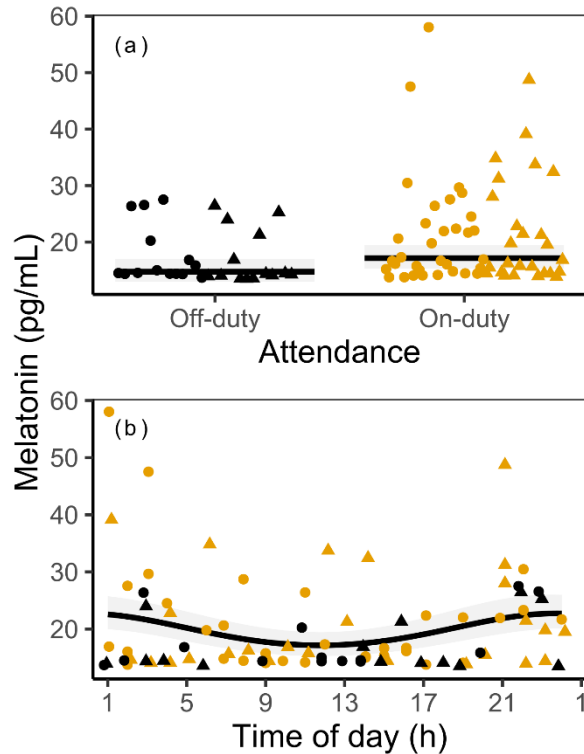
	Estimate	95% CI	t	P
intercept	0.36	0.34 to 0.37	49.2	< 0.0001
attendance: on-duty	-0.02	-0.04 to -0.003	-2.3	0.02
sine(time of day)	0.0009	-0.01 to 0.01	0.16	0.88
cosine(time of day)	-0.02	-0.03 to -0.005	-2.96	0.004

314

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315

316 **Figure 2. Melatonin's association with attendance behavior (a) and time of day (b).**

317 Solid lines and shaded areas represent the reverse-transformed predicted values and

318 95% credible intervals, respectively, from the top model. Circles and triangles represent

319 values from individual females and males, respectively, and the values are jittered

320 slightly along the x-axis to improve clarity by reducing overlap of individual values.

321 Lighter yellow points illustrate on-duty attendance, while darker black points illustrate

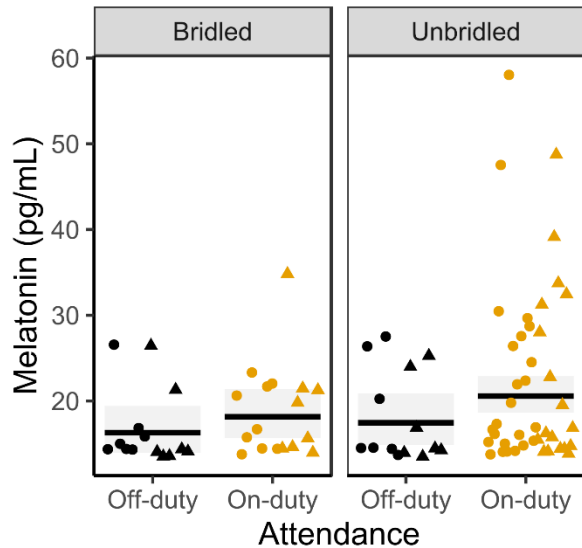
322 off-duty attendance.

323

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324

325 **Figure 3. Melatonin’s association with attendance behavior in bridled and**

326 **unbridled morphs.** Solid lines and shaded areas represent the reverse-transformed

327 predicted values and 95% credible intervals, respectively, from the model including the

328 **inter**action between attendance and morph (ER = 1.32). Circles and triangles represent

329 values from individual females and males, respectively. Lighter yellow points illustrate

330 on-duty attendance, while darker black points illustrate off-duty attendance.

331

332 *Corticosterone*

333 Neither our capture protocol nor if a bird was captured previously significantly influenced

334 baseline corticosterone (Supplementary Corticosterone Analyses). Ninety-three

335 individuals had information for all the predictors included in the saturated model. The

336 mean corticosterone concentration was 5.15 [4.36 to 5.93] ng/mL (median = 3.86

337 ng/mL, range = 1.21 to 21.63 ng/mL). The null model was the top model (Table 3).

338 Morph and time of day were nearly as likely (evidence ratios = 0.95 and 0.93,

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339 respectively) as the null model in predicting corticosterone concentration (Table 3).

340 Thus, both morph and time of day had limited ability to predict corticosterone

341 concentration (Fig. 4; Table 3).

342

343 **Table 3. Model results for corticosterone.** (a) Model selection table including the top

344 model, models testing our hypotheses, and the null model predicting corticosterone

345 concentration. (b) The model summary of the top models. “ER” is the evidence ratio of

346 the model to the null model following Burnham *et al.* (2011).

Dependent variable: Corticosterone

(a) Model selection list

Model parameter(s)	AICc	ΔAICc	ER
null	193.35	0	
morph	193.46	0.11	0.95
cosine(time of day) + sine(time of day)	193.50	0.15	0.93

(b) Summary of top models

<u>Null</u>	Estimate	95% CI	t	P
intercept	1.41	1.27 to 1.54	20.18	< 0.0001

Morph only

intercept	1.28	1.05 to 1.5	11.14	< 0.0001
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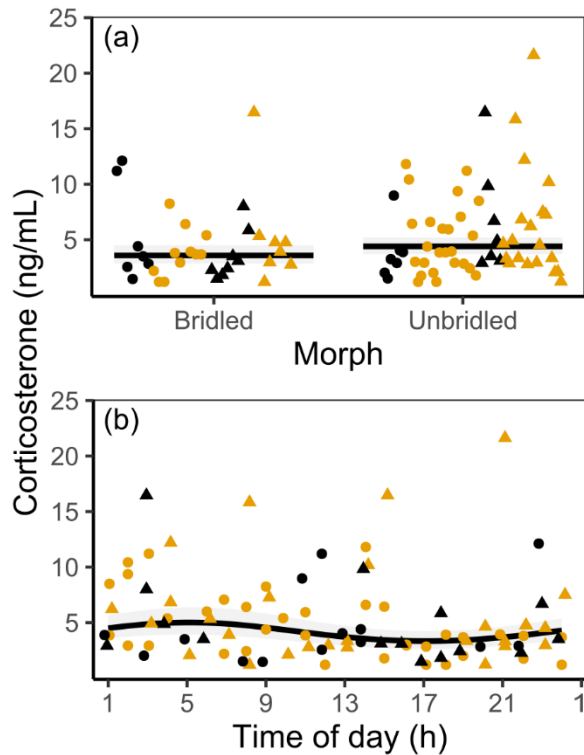
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morph	0.2	-0.08 to 0.49	1.42	0.16
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Time of day only

intercept	1.41	1.27 to 1.55	20.4	<0.0001
sine(time of day)	0.2	0.0005 to 0.39	2	0.05
cosine(time of day)	0.05	-0.14 to 0.23	0.49	0.62

347



348

349 **Figure 4. Corticosterone’s association with morph only and time of day only.** Solid
 350 lines and shaded areas represent the reverse-transformed predicted values and 95%
 351 credible intervals, respectively, from the models including either morph only (a) or time
 352 of day only (b). For (b), the values are jittered slightly along the x-axis to improve clarity

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353 by reducing overlap of individual values. Circles and triangles represent values from
354 individual females and males, respectively. Lighter yellow points illustrate on-duty
355 attendance, while darker black points illustrate off-duty attendance.

356

357 **Discussion**

358 Contrary to expectations, the common murre did not schedule their incubating and
359 brooding (on-duty attendance) by time of day and sex, highlighting the importance of
360 testing assumptions based on other populations or species. During the continuous light
361 of polar summer, common murre maintained diel variation in melatonin (Fig. 2b; Table
362 2), supporting our hypothesis that common murre can use melatonin to signal time of
363 day physiologically. Corticosterone, on the other hand, only had a weak tendency
364 towards a predictable diel profile (Fig. 4b; Table 3), suggesting that corticosterone may
365 not be an important signal of time of day during the continuous light of polar summer.
366 Morph explained variation in attendance behavior and melatonin (Fig. 1; Tables 1 & 2),
367 whereas the relationship between morph and corticosterone was less clear, with a
368 tendency towards a higher concentration in unbridled compared to bridled individuals
369 (Fig. 4a; Table 3).

370

371 *Colony attendance during polar summer*

372 Our results on attendance behavior differed from those reported in other studies on sex-
373 stereotyped timing of colony-based behaviors in common murre. Previously, the sexes
374 of common murre on Hornøya were described as feeding their chick at specific times

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375 of day, and this description was based on 11 mixed-morph pairs (Holmøy, 2019). Even
376 though chick provisioning and colony attendance may not follow the same schedule
377 across the diel cycle, the discrepancy between the current results and the sex-
378 stereotyped diel-pattern in chick provisioning may be explained by the behavior of
379 individual breeding pairs or the morph-composition of these pairs. Other charadriiforms
380 breeding under polar day had nest attendance rhythms that varied markedly among
381 breeding pairs, and these rhythms were not synchronized among pairs (Steiger et al.,
382 2013), illustrating that even if some pairs maintained sex-stereotyped diel-rhythms of
383 breeding-site attendance, no unified pattern would emerge at the population level.
384 Additionally, morph or the morph-composition of breeding pairs influences breeding
385 performance (Kristensen et al., 2014), behavior (Fig. 1; Table 1), and physiology
386 ((Tigano et al., 2018); Table 2) in common murre (discussed in detail below). Thus, the
387 current results provide a clear depiction of the general pattern of colony attendance
388 behavior at the population level in common murre breeding during polar summer. Note,
389 however, that our study was not designed to investigate diel rhythms of on- or off-duty
390 attendance at the colony within individuals or pairs (*sensu* (Huffeldt and Merkel, 2016)).
391 Morph composition of breeding pairs could be a determining factor of on-duty
392 attendance rhythms, and should be the focus of a systematic investigation of individual
393 rhythms of colony attendance in common murre during polar summer to understand if,
394 and how, traits linked to plumage color affect the ability of murre to track the diel cycle
395 during polar summer.

396

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397 *The role of melatonin and corticosterone during polar summer*

398 The ability of time of day to predict the variation of melatonin emphasizes its potential
399 role in providing a physiological signal of time of day under continuous light.

400 Contrastingly, the diel profile of corticosterone had limited variation across the polar
401 day, suggesting that diel rhythmicity in corticosterone may play a minor role, if any, in
402 signaling time of day under these extreme photic conditions. Even though polar summer
403 is characterized by continuous light, other environmental cues can be used by
404 organisms to track the 24-h diel cycle, including, among others, diel changes in light
405 intensity, spectral composition of sunlight, and temperature (Ashley et al., 2013; Huffeldt
406 et al., 2020; Williams et al., 2015). Common murrelets may be using one or more of these
407 environmental cues to synchronize their physiology to the diel cycle. Below, we discuss
408 the role of melatonin and corticosterone in keeping time under polar photic conditions.

409

410 The role of melatonin during polar day

411 Melatonin varied by time of day and between colony attendance behaviors (Fig. 2), and
412 the difference in melatonin levels between colony attendance behaviors was still
413 significant when time of day was accounted for (Table 2), indicating that behavior linked
414 directly to melatonin concentration. The on-duty birds had consistently higher
415 concentrations of melatonin regardless of time of day (Fig. 2). Elevated melatonin
416 during daytime in other species of birds was attributed to changes in behavioral states,
417 *i.e.*, from an active to a resting state (John et al., 1993; Tarlow et al., 2003), and this in

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418 combination with our result reveals that birds seem to behaviorally modulate melatonin
419 despite a well-lit environment.

420 The behavioral state of being on-duty could facilitate the accrual of the benefits of
421 melatonin, which is further supported by evidence that elevated melatonin promotes the
422 benefits of rest and sleep (Pandi-Perumal et al., 2006) and that common murre
423 primarily rest when attending the colony (Kappes et al., 2011). However, if the murre
424 were not resting or sleeping with their eyes closed or covered, then the perceived
425 illumination resulting from being alert under the continuous light could suppress
426 melatonin, resulting in low melatonin concentration in both on- and off-duty birds that
427 are alert and attending the colony.

428 Under this model, the lower light intensities during the night have a weaker
429 suppressive effect on melatonin than during daytime when the light intensity is at its
430 highest, resulting in the observed diel pattern in melatonin in birds attending the colony.
431 This model also suggests that melatonin concentration is not controlled directly by only
432 the circadian system, but is additionally or independently modulated by perceived light
433 intensity and behavior, which could explain the large amount of variation measured in
434 the diel profile of melatonin (Fig. 2). Therefore, our data indicate that common murre
435 can both track the 24-h day with melatonin and behaviorally modulate their melatonin
436 and its associated physiological benefits. This flexible melatonin response in common
437 murre may be widespread in polar-adapted vertebrates, because it provides a
438 mechanism by which polar inhabitants can benefit from melatonin under the continuous
439 light of polar summer. We encourage further research on polar vertebrates using

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440 experimental exposure to periods of darkness and investigation of potential pathways
441 allowing for behavioral modulation of melatonin.

442

443 The role of corticosterone during polar day

444 The common murre had limited diel variation in their corticosterone profile (Table 3;
445 Fig. 4). Low or absent diel variation in glucocorticoids is emerging as a common
446 phenomenon in polar birds and mammals, indicating that low-amplitude cycling or
447 invariable profiles of corticosterone provides advantages under the continuous light of
448 polar summer. Additionally, these combined results suggest that glucocorticoids either
449 play a minor role in internal timekeeping or that low-amplitude rhythms of
450 glucocorticoids are sufficient to fulfill their daily functions during the continuous light of
451 polar summer.

452 Sampling different individuals to reconstruct diel variation is a common approach
453 to investigate glucocorticoids during polar summer (*i.e.*, (Barrell and Montgomery, 1989;
454 Huffeldt et al., 2020; Steenweg et al., 2015; Vleck and van Hook, 2002); this study [*cf.*
455 (Scheiber et al., 2017)]). However, studies in which the same individuals are sampled
456 serially across the diel cycle would provide better resolution for assessing whether low-
457 amplitude, diel rhythms in glucocorticoids are more widespread than previously
458 described (*sensu* (Cockrem, 1991; Scheiber et al., 2017)). Additionally, experiments
459 that manipulate glucocorticoids in which diel variation is either abolished or established
460 will be fundamental to understanding the functional role that glucocorticoids play in the
461 diel activity and physiology of polar vertebrates.

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462

463 *Color dimorphism is associated with differences in behavior and physiology*

464 Color morph was the best predictor of colony attendance behavior and an important
465 predictor of melatonin, even though the effect size of morph was small in both instances
466 (Tables 1 and 2; Fig. 1; Supplementary Results). The importance of the interaction of
467 attendance and morph as a predictor of melatonin indicates the complex relationship
468 between physiology, behavior, and the plumage dimorphism (*i.e.*, Fig. 3). Higher
469 melatonin in on-duty, unbridled murrets could reduce activity and induce sleep (Hendel
470 and Turek, 1978; Hishikawa et al., 1969), which would result in them being more
471 stationary when on their egg or chick than bridled murrets, thereby explaining the higher
472 proportion of unbridled individuals being on-duty compared to bridled individuals (Fig.1).
473 Proximate mechanisms associated with differences in physiology (*i.e.*, melatonin) and
474 differential interaction with the environment via colony attendance behavior between
475 bridled and unbridled murrets may underlie the differences in breeding performance
476 described previously, further suggesting that the strategy employed by one morph
477 compensates for the strategy employed by the other morph (Kristensen et al., 2014).
478 Thus, differences in physiology and behavior between morphs may be the result of
479 balancing selection maintaining complimentary optima for traits in each morph.

480 Among other charadriiforms, male ruffs (*Philomachus pugnax*) have three
481 different plumage morphs, each associated with differences in reproductive strategy,
482 body size, and aggressive behavior, and the morphs and their associated traits are
483 linked to a complex structural genomic variant that facilitates the morphs' maintenance

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484 in the population (Küpper et al., 2016; Lamichhaney et al., 2016). Similarly, plumage
485 color morph, thermal adaptation, parental behavior, and hormone physiology appear
486 connected in Atlantic common murrets ((Birkhead, 1984; Kristensen et al., 2014;
487 Reiertsen et al., 2012); this study), and their association is probably maintained by
488 pleiotropy (*i.e.*, when one gene affects multiple traits), linkage between genes or their
489 regulatory elements, or a combination thereof (Tigano et al., 2018). Color
490 polymorphisms are associated with variation in seemingly unrelated traits, including
491 behavior and physiology, in a variety of species (Mckinnon and Pierotti, 2010), and this
492 study advances our understanding of the mechanisms enabling the maintenance of
493 color dimorphisms within populations by unveiling differences in behavior and
494 physiology between bridled and unbridled common murrets.

495

496 *Common and thick-billed murrets have different behavior and physiology during polar*
497 *summer*

498 Our results illustrate the contrasting behavior and physiology of common and thick-billed
499 murrets during the continuous light of polar summer. First, common murrets at polar
500 latitude had neither sex-stereotyped variation in their on-duty attendance nor a sex-
501 stereotyped diel profile in melatonin (Figs. 1, 2; Tables 1, 2), both of which contrasted
502 thick-billed murrets (*i.e.*, (Elliott et al., 2010; Huffeldt et al., 2020; Huffeldt and Merkel,
503 2016)). Second, common murrets also had a weak tendency towards diel variation in
504 their corticosterone profile, which was not found using the available data on thick-billed
505 murrets (Huffeldt et al., 2020). For these reasons, we discourage the direct comparison

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506 of common and thick-billed murre based on the assumption that the two species share
507 the same physiology and ecology in response to photic cues.

508 Thick-billed murre from another polar colony, Kippaku in Greenland, maintained
509 sex-stereotyped, diel variation in melatonin, and this variation was associated with a
510 sudden change in light intensity when their breeding cliff fell into shadow (Huffeldt et al.,
511 2020). We were unable to investigate if this phenomenon occurred in the common
512 murre on Hornøya, because the low elevation of the colony and the broad ledges
513 facing primarily Northwest meant that the study plots were not exposed to stark
514 transitions between full sun and shade. Note that as both sexes of thick-billed murre
515 could not be sampled across the complete diel cycle in Huffeldt et al. (2020), due to
516 thick-billed murre's sex-segregated rhythms of colony attendance, the results of these
517 two studies are not directly comparable.

518

519 **Conclusions**

520 We found that common murre maintain a diel profile in melatonin under the continuous
521 light of polar day and that they are probably modulating their melatonin concentration
522 behaviorally. Additionally, we found that corticosterone is unlikely to signal time of day
523 physiologically, which adds to the mounting evidence that glucocorticoids either play a
524 minor role or require a very low-amplitude rhythm to satisfy their physiological duties at
525 polar latitude. We found also that morph was a predictor of colony attendance behavior,
526 melatonin, and, to a more uncertain extent, corticosterone, and this provided additional

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527 support for the adaptive significance of traits linked to the plumage color dimorphism of
528 common murrelets in the Atlantic Ocean. We encourage additional research to elucidate
529 the mechanisms underlying differences in melatonin among on- and off-duty birds
530 attending the colony, individual rhythms of on-duty attendance during polar summer,
531 and the evolutionary processes resulting in the observed differences in behavior and
532 physiology among bridled and unbridled common murrelets.

533

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537 Trappschuh for assistance with the melatonin assay; and Juanita Olano Marin for
538 assistance with the corticosterone assay.

539

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541 supervision of K.E.E. and T.K.R., conducted statistical analyses, and drafted the
542 manuscript with A.T. W.G. assayed melatonin. S.J.-E. assayed corticosterone. T.M.
543 performed genetic sex-identification. All authors reviewed and revised the manuscript
544 critically.

545

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549 analysis, and interpretation of data; in the writing of the manuscript; or in the decision to
550 submit the article for publication.

551

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