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14

15 **Interactive effects of climate and forest canopy cover on Goshawk productivity**

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26 **ABSTRACT:**

27 In the current scenario of human-induced environmental changes, boreal forest biodiversity appears to be threatened by
28 both deforestation for timber production and climate change . A northern species which has experienced a decline due
29 to ongoing habitat degradation in Finland is the Northern Goshawk (*Accipiter gentilis*), a forest-dwelling avian predator
30 that inhabits mostly mature coniferous forests. In order to uncover possible interactive effects of climate and landscape
31 structure on this species, we tested whether temperature and precipitation affect Goshawk reproductive performance
32 differentially in closed (i.e. forest) or open (mainly forest-farmland mosaics) habitats, accounting for land cover at
33 different distances from nests (250m, 500m, 1000m and 2500 m). Long-term data on brood size and individual chick
34 weight were used to describe breeding success over a 14 year period. Brood size was negatively associated with March
35 and May temperature and positively with June temperature, but no trends related to landscape structure were identified.
36 Chick body condition was negatively affected by high forest cover closest to the nest (250m), but negative effects of
37 June precipitation on this variable proved to be significantly greater in open than in closed habitats, with results
38 consistent at different scales, i.e. precipitation had greater negative effects on chick body condition in open than in
39 closed landscapes. Precipitation is forecast to increase in the region as a result of climate change, hence forest cover
40 could exert a positive role in mitigating adverse effects of unfavorable climatic conditions. Outcomes of this study may
41 be used to inform sustainable timber harvest management strategies.

42

43 **KEYWORDS:**

44 *Accipiter gentilis*, reproduction, habitat, weather

45

46 **ACKNOWLEDGMENTS:**

47

48 INTRODUCTION

49 One of the fundamental objectives of current ecological research is to address how human-induced environmental
50 changes affect species population dynamics (Inger et al. 2014). Global biodiversity is facing serious declines (Butchart
51 et al. 2010) through multiple causes, although habitat destruction and degradation are thought to be key principle drivers
52 (Sala et al. 2000, Jetz et al. 2007). The world's forests are of great importance for the conservation of many threatened
53 species (Myers et al. 2000), but continuing high rates of constitute a major threat to biodiversity (FAO 2010). Whilst a
54 focus on conservation efforts has been on high biodiversity tropical forests (e.g. Fitzherbert et al. 2008, Gardner et al.
55 2009, Gibson et al. 2011), deforestation may also have serious consequences for biodiversity in the boreal zone, in
56 particular through effects of timber harvesting on forest specialist species (Schmiegelow & Mönkkönen 2002,
57 Mazziotta et al. 2016).

58 Over recent decades, climate change has also been recognized as a key threat to biodiversity. Ongoing climate change
59 has had many demonstrated effects on natural species populations (e.g. Ludwig et al. 2006, Virkkala et al. 2008,
60 Thackeray et al. 2016), and for many species, extinction risk will be higher in the future under scenarios of continued
61 global warming (Bellard et al. 2012). Effects of habitat loss and climate change are often not independent (Oliver &
62 Morecroft 2014). For example, impacts of climate are likely to be more severe in highly modified (e.g. Thomas et al.
63 2004) and/or highly fragmented (e.g. Opdam & Wascher 2004, Verboom et al. 2010) landscapes through effects on
64 dispersal and population persistence. Managing habitats, in particular to reduce fragmentation, may help populations to
65 persist in the face of climate change (e.g. Oliver et al. 2015). Despite the importance of these factors on population
66 trends, interactions between forest habitat and climate have been poorly studied (Virkkala 2016), having mainly
67 considered how reduced forest cover could prevent species tracking suitable climatic conditions under different climate
68 change scenarios (Hole et al. 2009, Araújo et al. 2011). Therefore, an exploration of the joint role of climate conditions
69 and habitat suitability is needed, especially for those species that can move through different habitat matrixes.

70 The Northern Goshawk *Accipiter gentilis* (hereafter Goshawk) is a forest-dwelling avian predator that inhabits mostly
71 mature coniferous forests which it requires for breeding, but which can successfully exploit open areas, i.e. agricultural
72 landscapes and urban areas, for hunting (Cramp & Simmons 1980, Kenward 1982, Rutz 2008). As an apex predator, its
73 presence is believed to maintain forest community structure and biodiversity (Burgas et al. 2014). Generally, Goshawk
74 territory occupancy and nesting success are correlated with a high coverage of primary habitat (i.e. mature coniferous
75 forest) within the home range (Finn et al. 2002, Björklund et al. 2015). However, the relationship between brood size
76 and habitat type in the boreal zone is unclear, and studies have reported inconsistent findings, with brood size positively

77 associated either with primary habitat (forest), secondary habitats (such as farmland; Byholm et al. 2007, Björklund et
78 al. 2015) and even built-up areas (Solonen 2008, Björklund et al. 2015). In addition, in Finland a higher partial brood
79 loss has been recorded in open habitat-dominated territories (i.e. bogs and fields), compared to forest habitats (Byholm
80 et al. 2007). While the species' main prey are distributed fairly evenly over landscape gradients, alternative prey
81 abundance changes with habitat type (Byholm et al. 2007, Lehikoinen et al. 2013) and therefore it has been claimed to
82 be a driver of the differences in partial brood loss between habitats. However, alternative prey abundance is usually
83 high in farmland (Smedshaug et al. 2002, Tornberg et al. 2009), and therefore additional mechanisms might be in place.
84 Goshawk reproductive success, in common with other raptor species (Newton 1998), is furthermore known to be
85 influenced by weather conditions. Specifically, cold and wet springs and early summers have negative effects acting on
86 different stages of the breeding cycle, e.g. heavy rain may lower the likelihood of attempting to breed, decrease parent
87 foraging success and reduce nestling survival (Kostrzewa & Kostrzewa 1990, Bloxton 2002, Fairhurst and Bechard
88 2005, Moser & Garton 2009).

89

90 Here, we conduct the first study aimed at evaluating the role of forest cover in influencing climate effects on the
91 Goshawk in Finland, where the population trend has shown a slight but steady decline since the 1980s (Honkala et al.
92 2014). In particular, we tested whether temperature and precipitation affected Goshawk reproductive performance
93 differentially in closed (i.e. forest) or open (mainly forest-farmland mosaics) habitats, by means of multivariate
94 modeling of breeding output in terms of brood size and nestling body condition. We assumed that chick body condition
95 is a good measure of reproductive performance, supported by the fact that poor body condition in nestlings is likely to
96 reduce their survival during winter (Van der Jeugd & Larsson 1998, Newton et al. 2016), especially when considering
97 that young undertake autumn dispersal in their first year (Byholm et al. 2003). We expected that nests located in closed
98 canopy areas can support greater brood size and/or better chick body condition compared to those located in open areas,
99 thanks to the ability of forest to offer shelter to both Goshawks and their prey in adverse weather conditions.

100

101

102 MATERIALS AND METHODS

103 *Goshawk data*

104 Data on Goshawk brood size and individual chick body condition (based on individual chick weight), were used as
105 proxies for reproductive success. The data were derived from the Finnish National Ringing Scheme and consisted of
106 Goshawk ringing data at a national level (Finland lying approximately between 60° and 70° N, and 20° and 32° E),

107 spanning the years 1997-2014. The dataset was organized according to individual ringed nestlings (n = 14.664), to
108 which a series of parameters was linked: gender, wing length and weight, hatching day (Julian days), brood size, year
109 and location (the geographic coordinates of each nest having been recorded). Gender was determined based on foot
110 span and/or tarsus length, which both differ significantly between sexes from an early age (Hardey et al. 2006). Ringing
111 takes place during the first two-three weeks of June, when typically a substantial part of chick growth has already
112 occurred and therefore sex identification is possible. Additionally, in this phase chicks are still young enough not to
113 fledge prematurely due to the presence of the ringer. Brood size modeling required prior data rearrangement, and
114 singular broods were displayed as records (n = 7.473 broods). In doing so, hatching date of a brood was defined as that
115 of the first hatched in the brood, and was calculated by subtracting estimated age (see Appendix for age estimation)
116 from date of ringing. Broods lacking hatching date for one or more chicks were omitted.

117

118 Goshawk chicks were ringed, weighed and measured during the same period in June, but chick age at ringing varied
119 between and within broods. Skeletal growth is generally constant in nestling birds, while body weight varies in relation
120 to body condition (and hence usually food supply). In particular, in Goshawk, wing length is a skeletal measure that
121 varies little between sexes, contrary to other skeletal measures. Therefore it can be used to effectively control for
122 variation in age at ringing when modeling body condition (Hardey et al. 2006). Therefore, weight was standardized in
123 relation to size by modeling a growth curve of weight against wing length (see below).

124

125 *Climate data*

126 The climate data were provided by the Finnish Meteorological Institute and contained information in the form of daily
127 precipitation and temperature values referred to a national grid of 10x10 km cells. The data were modified so as to
128 obtain monthly mean temperature and monthly cumulative precipitation for each grid cell. Only the months believed to
129 be strictly related to the reproductive cycle (Fairhurst & Bechard 2005, Moser et al. 2009) were kept, that is from
130 February to June. In fact, in Fennoscandia Goshawks start displaying approximately in March while roughly all
131 nestlings have fledged by the end of June (Hardey et al. 2006, Valkama personal obs.). Nest locations that were within
132 a given 10-km² grid cell were assigned the derived climate variables for that grid cell.

133

134 *Landscape analysis*

135 Landscape analysis was conducted using Esri ArcGIS Desktop version 10.3, to obtain information about the
136 environment surrounding each nest based on land cover types as defined by CORINE Land Cover, level 1 . Nests were

137 projected on different CORINE Land Cover maps, with a resolution of 25 m (coordinate system EUREF-FIN, ETRS89)
138 in three different time periods, in order to account for land cover changes over the study period. Each of the land cover
139 maps from 2000, 2006 and 2012 were matched respectively with Goshawk data from 1997-2002, 2003-2008 and 2009-
140 2014. Nest records whose distance from any forest type exceeded coordinate accuracy (100 m) were assumed to be
141 errors and were omitted, since Goshawks require forested habitat for breeding (Cramp and Simmons 1980).
142 Subsequently, a buffer was created around each nest at 250m, 500m, 1000m, and 2500m distance (Fig. 1) in order to
143 assess effects at different scales of Goshawk home range (see Windén 1989, Finn et al. 2002, Byholm et al. 2007,
144 Björklund et al. 2015), and the area of each land cover type was extracted at each of the four scales. Although
145 Goshawks tend to prefer coniferous forest, they can also make use of deciduous or mixed forests. As we were primarily
146 concerned with overall habitat structure, rather than the tree species composition, we considered overall forested area.
147 The proportion of forest cover was defined as ‘closed canopy’ and all other habitats were combined and defined as
148 ‘open habitat’. The twelve files (three time periods for each of four buffer distances), derived by GIS analysis, were
149 merged together according to buffer radius to create four datasets spanning the period 1997-2014.

150

151 *Statistical modelling*

152 All statistical analyses were conducted in the R environment, version 3.1.2 (R Development Core Team 2015). To
153 investigate the interactive effects of weather and habitat closure on brood size and body condition, we used generalized
154 mixed-effects models (GLMM, specifying a Poisson distribution) and linear mixed-effects models (LMM, normal
155 distribution), respectively. Definition of the random factors was based on the knowledge that Goshawk nests can be
156 used for several years by the same pairs (Cramp & Simmons 1980), so year and nest site were defined as random
157 factors in both brood size and body condition models. The inclusion of year allowed to account for variation in
158 unknown parameters that are likely to fluctuate on an annual basis (e.g. prey availability). In addition, for body
159 condition, brood identity (i.e. a particular nesting attempt in a given year at a given site) was also specified as a random
160 factor to account for non-independence of individual chicks within a given brood.

161

162 Chick body condition was estimated by deriving residuals from a growth curve (e.g. REF). To construct the growth
163 curve, a Linear Mixed Model was used relating chick weight to chick age in days, including year and nest identity as
164 random effects. Three different models to describe the growth curve (linear, quadratic and asymptotic) were compared
165 via the Akaike Information Criterion (AIC) and the one with the lowest AIC value, the quadratic model, was selected
166 (Appendix 1). Residuals from the fitted regression line from this model (Fig. 2) were then used in the analysis as a

167 measure of chick body condition, i.e. chicks with negative residuals were lighter than expected for a given body size,
168 and chicks with positive residuals were heavier than expected. Henceforth these residuals are referred to as ‘body
169 condition’. The sex of the chick was included as a predictor variable when modeling body condition, rather than
170 including it in the growth curve model, as we were interested in the extent to which sex affected the relationship
171 between body condition, canopy cover and climate given that previous studies have identified different responses to
172 environmental variables between chicks of different sex (Byholm et al. 2002a, Byholm et al. 2002b),. After deriving the
173 body condition from the growth curve, we developed a preliminary model to identify possible confounding factors
174 influencing nestlings’ body condition, including sex, brood size, hatching date, latitude, longitude and the interaction
175 between hatching and latitude. All other statistical methods were analogous for brood size and body condition and are
176 explained in detail in the following paragraphs.

177

178 Goshawk reproductive success was analyzed following a standard protocol. Initially, effects of temperature,
179 precipitation and habitat cover were modelled separately in order to assess their individual contributions. For each of
180 these three initial models, the first step was to identify a subset of variables that showed some association with
181 Goshawk productivity and which had a low degree of intercorrelation. A list of all variables tested is shown in Table 1.
182 Collinearity between variables was tested by means of Variance Inflation Factors (VIF) and general trends observed
183 from pairwise scatterplots (Zuur et al. 2009). Variables with a VIF > 3.0 were sequentially removed until all remaining
184 variables had VIF < 3.0 (following Zuur et al. 2009). All variables included in the models were centered to have a mean
185 of zero before analysis, and scaled to allow the comparison of effect sizes of variables and therefore of model estimates.

186

187 Following reduction of the predictor variable data set, each of temperature, precipitation and closed canopy variables
188 selected were analysed in relation to brood size and body condition. Each model also included latitude, longitude and
189 hatching date. For body condition, brood size and sex were also included in the models (see above), as Goshawk
190 females are larger than males from an early age (Hardey et al. 2006). Stepwise model reduction was applied to each
191 model (temperature, precipitation and land cover) to achieve a Minimum Adequate Model (MAM). Land cover variable
192 models were computed for each of the four different scales. Therefore, at the end of this process, there were separate
193 MAMs for temperature, precipitation and for land cover at each of the four scales considered. Potential spatial
194 autocorrelation was tested by producing variograms derived from model residuals and the locations of each site using
195 the gstat package following the approach of Zuur et al. (2009). There was no evidence of spatial dependence in the
196 variograms (Appendix 1), therefore there was no need to account for spatial autocorrelation in the models.

197

198 The final step was to produce a model combining temperature, precipitation and land cover. Variables from each
199 separate MAM were combined and subject to further reduction according to VIF, and a final combined model was then
200 derived, again taking the minimum adequate model approach. Interactions between closed canopy and climate variables
201 (if in the final model) were analysed to specifically test for differences in climate responses in terms brood size and
202 body condition in relation to the degree of closed canopy.

203

204

205 RESULTS

206 *Brood size*

207 A negative correlation was identified between brood size and hatching date, with brood size significantly smaller for
208 late hatched broods ($r = -0.32$, $df = 7471$, $P < 0.001$). Hatching date was therefore included in all subsequent models to
209 distinguish its effect on brood size from that of climate variables. There was no evidence of any effects of latitude ($P =$
210 $n.s.$) nor longitude ($P = n.s.$) on brood size.

211

212 In landscape models, there was no evidence that brood size was influenced by habitat. Closed habitat cover was not
213 significantly correlated with brood size at any of the scales considered ($P = n.s.$). In climate models, no significant effect
214 of any precipitation variable was detected. Conversely, for temperature, the MAM contained significant negative effects
215 of March ($Z = -4.23$, $P < 0.001$) and May temperatures ($Z = -3.02$, $P = 0.002$) and positive effects of June temperature
216 ($Z = 4.08$, $P < 0.001$). Combined models did not result in any significant interaction between weather and landscape
217 variables for brood size, nor an effect of land cover, therefore the MAM for the combined model was the same as that
218 for the temperature model (Table 2).

219

220 *Body condition*

221 All variables included in the preliminary model were significant and therefore were included in subsequent models.
222 Females, as expected, had higher body condition than males ($t = -186.55$, $P < 0.001$). Furthermore, body condition
223 decreased at higher brood sizes ($t = -4.48$, $P < 0.001$), and increased with later hatching dates ($t = 3.36$, $P < 0.001$), at
224 greater latitudes (i.e. more northerly, $t = 2.78$, $P = 0.005$), and at greater longitudes (i.e. more easterly, $t = 3.66$, $P <$
225 0.001). There was also a significant interaction between hatching and latitude ($t = -5.07$, $P < 0.001$).

226

227 In landscape models, closed habitat cover was significantly associated with body condition only at the smallest scale
228 (250m), where higher closed canopy was associated with lower body condition (250 m: $t = -2.09$, $P = 0.036$). Among
229 climate variables, body condition was negatively associated with June precipitation ($t = -4.43$, $P < 0.001$). There was no
230 significant effect of any temperature variable on body condition. Final combined models, including significant climate
231 variables and closed habitat cover, showed a significant interaction between June precipitation and closed habitat at all
232 scales (250 m: $t = 2.64$, $P = 0.008$; 500 m: $t = 2.46$, $P = 0.014$; 1000 m: $t = 2.07$, $P = 0.038$; 2500 m: $t = 2.01$, $P = 0.044$),
233 although this was most pronounced at the smallest scale (Table 3). This interaction showed that body condition declined
234 with increasing precipitation in both open and closed canopy locations, but that the rate of decline was steeper in open
235 habitats. This is illustrated in Fig. 3, where the dataset was divided into two using mean closed canopy as a threshold to
236 identify two data subsets (open and closed canopy), and the model was re-run on each subset (excluding closed canopy
237 variable; details of combined models and figures at the other scales are given in [Appendix 2](#)). There was also a
238 significant interaction between latitude and hatching date, and between sex and June precipitation (Table 3). The former
239 showed that earlier hatched chicks had lower body condition at higher latitudes, while the latter indicated a different
240 response between males and females to June precipitation in that there was a significant decrease in females body
241 condition with an increase in June precipitation, while there was no significant effect in males.

242

243

244 All four combined models had a marginal R squared of approximately 0.68 and a conditional R squared of 0.76, thus
245 showing they accounted for a high percentage of variation in the data. However, this variation was mainly explained by
246 fixed factors (marginal R squared), and a minor improvement was earned by including random factors (conditional R
247 squared).

248

249

250 DISCUSSION

251 Our original expectation, that Goshawk nests in closed canopy habitats would be buffered from potentially negative
252 effects of weather, was partially supported in that there was no effect for brood size, but precipitation had a less
253 negative effect on body condition when there was a high proportion of closed canopy in the surrounding habitat.
254 Furthermore, this effect was not dependent on the scale of habitat resolution, being consistent at the four scales
255 considered.

256

257 *Brood size*

258 No effect of closed canopy on the number of chicks produced in a brood was detected, similarly to Björklund et al.
259 (2015), but conversely to Byholm et al. (2007). However, the mean proportion of closed canopy at the different scales
260 considered was quite high (250 m: 90.27%; 500 m: 85.48%; 1000 m: 80.71%; 2500 m: 73.47%). It may be that a
261 negative effect of reduced primary habitat (closed canopy) on brood size would not be evident above a certain
262 threshold, which on average might not be reached in Goshawk territories in Finland. Brood size was negatively
263 associated with March and May temperatures and positively with June temperature. The negative associations with
264 March and May temperatures might seem counterintuitive. However, spring temperature increment is claimed to
265 advance breeding more in prey species than in predators (Nielsen and Moller 2006, Both et al. 2009). This in turn could
266 cause a mismatch in predator-prey phenologies later in the season, when more resources are needed for chick rearing.
267 Such an effect could cause spring temperature to be negatively associated with brood size. Indeed, there is little
268 evidence of advances in Goshawk hatching date with climate warming (Lehikoinen et al. 2013), while on the contrary it
269 has been reported as a long term response in a prey species, the black grouse *Tetrao tetrix* (Ludwig et al. 2006).
270 The effect of lower June temperatures are likely to be related to a decrease in offspring survival, as cold temperatures
271 during the rearing period could reasonably expose chicks to hypothermia (Newton 1998, Lehikoinen et al. 2013). This
272 might be especially well pronounced at high latitudes, such as in Finland. There was no evidence for an effect of
273 precipitation in our study, although Lehikoinen et al. (2015) found that Goshawk brood sizes were negatively related to
274 June precipitation.

275

276 *Body condition*

277 There was an unexpected negative effect of a high proportion of closed canopy cover on body condition at the smallest
278 scale considered. We propose two possible ecological processes which may underlie this result. First, in forest habitats
279 snow cover is prolonged in spring compared to open habitats, which could affect predation success, for example
280 through facilitating more efficient antipredator strategies by grouse (Marjakangas 1990, Tornberg et al. 2012), when
281 alternative prey are not yet available. Second, later in the season, territories that are particularly homogenous in terms of
282 forest cover could lack the species richness of alternative prey provided by forest edges, as suggested in Kudo et al.
283 2005 (also Krüger and Lindström 2001), and where they could still put into practice their typical hunting technique of
284 ambushing the prey from a concealed perch (Cramp and Simmons 1980).

285

286 Among weather variables, only June precipitation affected nestling body condition, which was lower when conditions
287 were wetter. High summer rainfall may have a number of negative effects, for example reducing prey availability and
288 suppressing hunting behavior or lowering the ratio between benefits and costs of hunting (Kostrzewa & Kostrzewa
289 1990, Newton 1998, Bloxton 2002). In addition, in such weather conditions more energy is required for
290 thermoregulation and brooding of the chicks (Katzenberger et al. 2015).

291

292 The combination of climate and landscape variables for body condition followed our initial expectation in that there
293 were significant interactive effects of June precipitation and closed habitat at all scales, showing that the decrease in
294 chicks body condition due to strong rainfall was reduced where the proportion of closed canopy was high. This suggests
295 a role of forest cover in diminishing negative effects of adverse weather. The significance of the interaction was
296 maintained at all scales, but it was stronger at the smallest scale. This suggests that the interactive effect of closed
297 canopy and climate could be exerted at two levels: (i) at all scales, indirectly, modifying the parents' foraging behavior
298 by making hunting in open habitat more difficult than in closed; furthermore there would be less shelter for prey species
299 that would result in a low level of prey activity and thus detection by the Goshawk; (ii) at a nest site scale, acting
300 directly on nestling body condition especially where shelter, offered by a closed canopy vegetation, is poor. However,
301 this second explanation relies on the assumption of a correlation between closed canopy cover at the 250m scale and
302 shelter at the nest site - further research including finer scaled habitat data would be required to test this assumption.
303 However, such an effect is not unprecedented in raptors –similar differential precipitation effects have been found in
304 nesting Peregrine Falcons *Falco peregrinus* in Australia, where pairs with sheltered cliff-ledge nest-sites bred as well in
305 wet years as in dry ones, whereas those with exposed sites often failed in wet years (Olsen & Olsen 1989).

306

307 Two other interactions that significantly affected chick body condition were identified: hatching date and latitude, and
308 June precipitation and sex. Hatching date can significantly affect chick body condition at higher latitudes, where late
309 hatched chicks are in better condition, while in the south, chick body condition is independent of hatching date. This
310 result is ecologically reasonable as nestlings in the south hatch when the climate is relatively stable compared to the
311 north of Finland. Additionally, later hatching in the north might be better synchronised with the arrival of migrating
312 prey species. We also found that females and males responded differently to climate variables, females tending to lose
313 weight more strongly than males when June precipitation was higher. It might be possible that females, being
314 significantly larger, require a higher food intake which cannot be fulfilled in adverse weather conditions, leading to
315 greater weight loss.

316

317 *Caveats*

318 We considered only two aspects of reproductive success, brood size and nestling body condition. These data included
319 records only from successful breeding events, so we were unable to assess patterns of complete or partial nesting failure
320 linked to landscape features or weather conditions. Additionally, data on snow cover in open and closed canopy was not
321 available, even though different melting patterns in relation to the extent of canopy closure could influence prey
322 detectability, and hence adult body condition and, especially for snow cover in early spring, chick body condition. The
323 database of the Finnish Ringing Scheme does not include estimates of partial brood loss (due to starvation or
324 cannibalism), so a consideration of this aspect of reproductive success, in particular in relation to snow cover in early
325 spring, would require dedicated intensive monitoring of Goshawk nests, which would nevertheless be a worthwhile
326 research area to pursue

327

328 The Goshawk occupies territories according to the Ideal Pre-emptive Distribution (Krüger & Lindström 2001), typical
329 of territorial species, and therefore the question of whether lower fitness pairs (i.e. young and low quality pairs) are
330 misplaced towards less suitable habitat arises. However, it could conversely be that the pattern studied is hidden by this
331 behavior as heterogeneous habitats seem to be generally profitable, and so pairs with better skills to cope with adverse
332 conditions might occupy them. Nevertheless, knowledge of the adults, and the influence of their age or 'quality' on
333 reproductive outputs, would be an interesting addition to this research area.

334

335 **Conclusions**

336 We found that forest cover (as measured by closed canopy extent) plays a positive role in mitigating adverse effects of
337 unfavorable climatic conditions on Goshawk reproductive performance. We also found that brood size was larger in
338 warmer springs. Temperatures are predicted to increase in Finland (REF), which may benefit Goshawks in terms of
339 brood size. However, total precipitation is also predicted to increase (Jylhä et al. 2004, IPCC 2014), which has negative
340 effects on chick body condition, especially for females. Given the interactive effect of climate and forest cover on body
341 condition found in this study, such negative effects are likely to be ameliorated by high forest cover. In the same way, a
342 combined effect of increased precipitation and increased timber harvesting could lead to negative effects on Goshawks
343 in the boreal region. Strategies that promote resilience to climate change (the capacity to absorb disturbance and recover
344 from its effects) are becoming key goals in terms of minimizing potentially harmful impacts on biodiversity (Morecroft
345 et al. 2012). In the case of the Goshawk, our results strongly suggest that resilience (*sensu* IPCC 2007) to climate

346 change will be increased by maintaining forest cover due to its role in lessening the negative effects of precipitation on
347 chick body condition. We stress, however, that there is the need for further research conducted at a local scale, which
348 would allow to control for possible confounding factors, such as variations in alternative prey availability across the
349 landscape.

350

351

352

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487 **FIGURES**

488 **Fig 1** Distribution of Goshawk nests visited by ringers in Finland in three periods 1997-2002, 2003-2008 and 2009-
489 2014, and an example of the buffering method used to analyse land cover at different scales in the breeding sites
490 (bottom right). The central black dot represents the nest location and the surrounding concentric circles show the
491 different scales considered in the analysis (250m, 500m, 1000m, and 2500m).

492 **Fig 2** Scatter plot of body weight against wing length (both variables are centered and scaled). The regression line,
493 representing the growth curve, is shown with 95% confidence intervals.

494 **Fig 3** Body condition index against June precipitation index in closed (forest canopy $\geq 50\%$) and open ($< 50\%$) habitats
495 (250 m scale). Graphs for scales 500m, 1000m and 2500m are reported in Appendix 2

496 **Fig 4** Body condition index against June precipitation index in closed (forest canopy $\geq 50\%$) and open ($< 50\%$) habitats
497 (500 m scale).

498 **Fig 5** Body condition index against June precipitation index in closed (forest canopy $\geq 50\%$) and open ($< 50\%$) habitats
499 (1000 m scale).

500 **Fig 6** Body condition index against June precipitation index in closed (forest canopy $\geq 50\%$) and open ($< 50\%$) habitats
501 (2500 m scale).

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504 **TABLES**

505 **Table 1** General set of variables included in initial models for brood size and body condition. Significant variables
 506 selected through stepwise reduction were then included in final combined models as shown in Table 2 and Table 3.

Dependent variables	Explanatory variable tested	Random factor	Distribution
Brood size	Hatching date Feb to June temperatures and precipitation Latitude, Longitude Closed habitat	Nest ID Year	Poisson
Body condition	Sex Brood size Hatching date Feb to June temperatures and precipitation Latitude, Longitude Closed habitat	Nest ID Brood ID Year	Gaussian

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509 **Table 2** The effects of temperature, precipitation and closed habitat cover on Goshawk brood size. A minimum
 510 adequate model was derived by sequentially deleting non-significant terms (no land cover or precipitation variables
 511 were included in the final model). Model estimates and significance tests were based on a Poisson mixed model, which
 512 included year and nest site as random effects. All variables included in the models were scaled and centered to have a
 513 mean of zero before analysis. Since no land cover variable is included, estimates are relevant to all scales.

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Fixed effects	Estimate	St. Error	Z value	Pr(> z)
Intercept	1.0396	0.0081	127.35	<0.001
Hatching date	-0.1095	0.0074	-14.69	<0.001
March temp	-0.0344	0.0081	-4.23	<0.001
May temp	-0.2415	0.0080	-3.02	0.0025
June temp	0.0324	0.0079	4.08	<0.001

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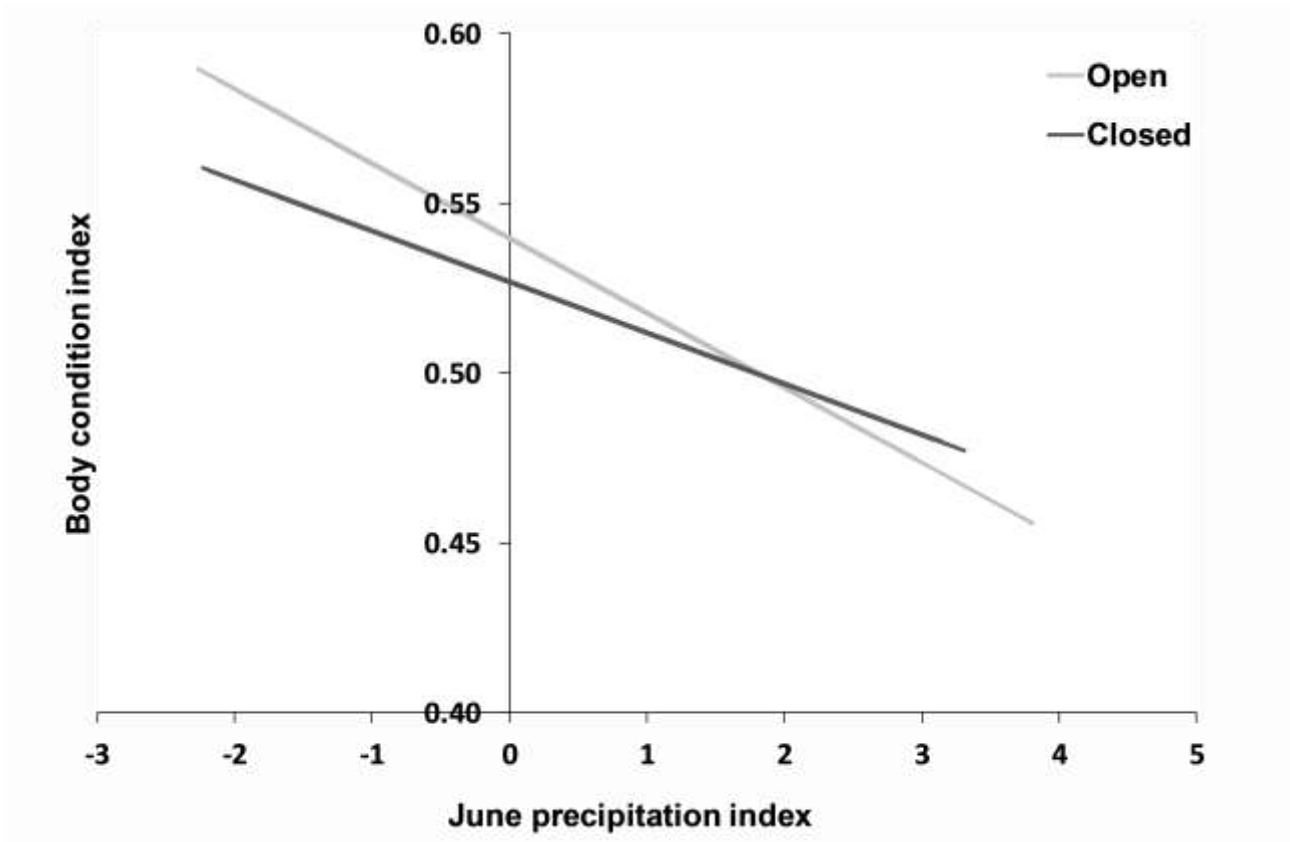
516 **Table 3** The effects of temperature, precipitation and closed habitat cover on Goshawk nestling body condition at scale
 517 250m. A minimum adequate model was derived by sequentially deleting non-significant terms. Estimates and
 518 significance tests were based on a linear mixed model, which included year, nest site and brood identity as random
 519 effects. All variables included in the models were scaled and centered to have a mean of zero before analysis. Sex was a
 520 two-level categorical variable (male and female), where the fixed effects are expressed male relative to female. Results
 521 for other scales are reported in Appendix 2.

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Fixed effects (250m)	Estimate	St. Error	T value	Pr(> z)
Intercept	0.5299	0.0052	100.8768	<0.001
Sex (male)	-1.0005	0.0054	-186.6939	<0.001
Brood size	-0.0158	0.0034	-4.5909	<0.001
Latitude	0.0106	0.0043	2.4576	0.014
Longitude	0.0180	0.0039	4.6447	<0.001
Hatching date	0.0118	0.0034	3.4639	<0.001
Closed canopy	-0.0071	0.0036	-1.9706	0.048
Hatch.*lat.	-0.0170	0.0033	-5.1502	<0.001
June prec	-0.0272	0.0045	-6.0018	<0.001
June p.*closed c.	0.0098	0.0035	2.7917	0.005
Sex*June prec	0.0217	0.0053	4.0501	<0.001

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