

1 **Winter territoriality and its implications for the breeding ecology of White-**
2 **throated Dippers *Cinclus cinclus***

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17 **Summary**

18

19 **Capsule:** Pairs of White-throated Dippers *Cinclus cinclus* which defended winter territories
20 bred earlier than non-territorial individuals, but there was no difference in reproductive
21 success.

22 **Aims:** The effect of winter territoriality on breeding ecology has rarely been studied in
23 resident birds. We carried out a preliminary investigation of whether winter territorial
24 behaviour and territory size affect the timing of reproduction, breeding territory size and
25 reproductive success in a riverine bird, the White-throated Dipper.

26 **Methods:** We monitored an individually marked population of White-throated Dippers in the
27 UK. Wintering individuals were classified as either territorial or ‘floaters’ according to their
28 patterns of occurrence and behaviour, and their nesting attempts were closely monitored in
29 the subsequent months. Winter and breeding territory sizes were measured by gently
30 ‘pushing’ birds along the river and recording the point at which they turned back.

31 **Results:** All birds defending winter territories did so in pairs, but some individuals changed
32 partners before breeding. Territorial pairs that were together throughout the study laid eggs
33 significantly earlier than pairs containing floaters and those comprising territorial birds that
34 changed partners. However, there were no significant differences in clutch size, nestling mass
35 or the number of chicks fledged. There was no relationship between winter territory length
36 and lay date or any measure of reproductive success, although sample sizes were small.
37 Winter territories were found to be significantly shorter than breeding territories.

38 **Conclusion:** Winter territoriality may be advantageous because breeding earlier increases the
39 likelihood that pairs will raise a second brood, but further study is needed. Territories are
40 shorter in winter as altitudinal migrants from upland streams increase population density on
41 rivers, but this may also reflect seasonal changes in nutritional and energetic demands.

42 **Introduction**

43

44 Territoriality, the defence of a distinct area from conspecifics, is a widespread and well-
45 studied behaviour in birds. Territories are usually secured for reproductive purposes and
46 provide individuals with exclusive access to limited resources, such as nesting sites or food
47 (Brown 1964, Maher & Lott 2000). The quality of an individual's territory is often a major
48 determinant of mate choice (e.g. Alatalo *et al.* 1986, Eckerle & Thompson 2006) and
49 reproductive success (e.g. van de Pol *et al.* 2006, Sergio *et al.* 2009b), and most field studies
50 of territoriality have therefore focused on the breeding season. By contrast, relatively little is
51 known about the fitness consequences of territoriality at other times of the year.

52 Territorial behaviour during winter has been documented in a variety of birds (Pulliam
53 & Millikan 1982, Snow & Snow 1988, Cuadrado 1997). In some species, individuals
54 establish a territory in order to monopolise a particular food source (Salomonson & Balda
55 1977, Snow & Snow 1988, Kelsey 1989). In others, it is thought that foraging strategies are
56 sufficiently diverse to enable individuals to remain in a limited area and defend it
57 economically (Brown 1964, Holmes *et al.* 1989, Salewski *et al.* 2002). Consequently, the
58 overwinter survival of individuals which do not or cannot defend a territory may be reduced
59 due to lower food availability or the costs associated with covering greater distances to feed
60 (Jenkins *et al.* 1963, Holmes *et al.* 1989, Cuadrado 1995). In a study of wintering European
61 Robins *Erithacus rubecula*, the feeding rates and body condition of territory holders were
62 similar to those of non-territorial birds, but the former were able to feed in less exposed sites,
63 suggesting that territories provided refuge from predators rather than access to food
64 (Cuadrado 1997).

65 Winter territories are sometimes defended by birds in pairs or groups and this must
66 offer fitness benefits to offset the costs of intraspecific competition for local resources. In

67 Mute Swans *Cygnus olor*, established pairs may maintain winter territories to ensure access
68 to high quality breeding sites and prevent rivals from taking over the area (Scott 1984). In
69 other species, pairs are formed during the autumn and defend a winter territory, either as a
70 single pair or collectively in groups, before breeding together (e.g. Logan & Hyatt 1991,
71 Hogstad 2014), and early pair bond formation may increase reproductive success (Fowler
72 1995). However, it has been shown in other species that individuals which defend a winter
73 territory as a pair are unlikely to breed together and instead may benefit from reduced
74 energetic expenditure associated with defence or increased rates of detecting rivals and
75 predators (Davies & Houston 1981, Gwinner *et al.* 1994). Further work is needed to
76 understand this variation in winter territorial strategies within and between species. In
77 particular, very few studies have investigated the consequences of winter territoriality for the
78 subsequent breeding season; the quality of winter territories in long-distance migrants is
79 known to have so-called ‘carry-over effects’ on the timing and success of reproduction
80 (Norris *et al.* 2004, Paxton & Moore 2015), but little is known about similar effects in species
81 which remain in the same area throughout the year.

82 White-throated Dippers *Cinclus cinclus* (hereafter ‘Dippers’) are aquatic songbirds
83 found almost exclusively along rivers and streams where they feed on freshwater
84 invertebrates and sometimes small fish (Tyler & Ormerod 1994). They provide an ideal
85 system for studying winter territoriality because their territories are linear and therefore
86 simple to survey and measure (D’Amico & Hemery 2003, Feck & Hall 2004, Chen & Wang
87 2010), but also because individuals vary in whether or not they defend a territory outside of
88 the breeding season. Dippers are strongly territorial when breeding, but while some birds are
89 thought to defend a territory throughout the winter, often in pairs, other individuals
90 apparently become ‘floaters’ and are mobile, foraging in a territory until being evicted when
91 encountered by the territory holder (Cramp 1988, Tyler & Ormerod 1994). Furthermore,

92 birds breeding on upland streams often descend onto rivers in the winter where they compete
93 for territories with local residents (Tyler & Ormerod 1994). However, the consequences of
94 variation in winter territorial behaviour for reproductive success in the following season have
95 never been studied.

96 Holding a territory in the winter may allow individuals to enter the breeding season in
97 better condition, which may in turn lead to earlier or more successful reproduction. Dippers
98 breeding earlier in the season typically have larger clutches, larger broods and are more likely
99 to raise a second brood (Tyler & Ormerod 1985, Ormerod & Tyler 1993, Wilson 1996),
100 although offspring survival may be lower in early broods and second broods (Ormerod &
101 Tyler 1993). The size of the winter territory and whether or not it is defended by a pair may
102 also impact on the timing and success of reproduction, especially if territorial pairs are future
103 breeding partners. We test these hypotheses using field observations of an individually
104 marked population of Dippers to (1) quantify winter territorial behaviour and determine
105 whether territorial pairs are future breeding partners; (2) compare the timing of breeding and
106 reproductive success between winter territory holders and floaters; (3) investigate the
107 relationship between winter territory size and breeding territory size; and (4) investigate the
108 relationship between winter territory size and the timing of breeding and reproductive
109 success.

110

111 **Methods**

112

113 *Study site and winter surveys*

114 We monitored a population of Dippers in the River Lune catchment within four miles of
115 Sedbergh, Cumbria, UK (54.3236° N, 2.5282° W), between January and July 2016. This
116 population of 40-50 breeding pairs has been individually marked and intensively studied
117 since 2013. Each year, all unringed birds are caught in mist nets or in hand nets placed over
118 the nest and fitted with a British Trust for Ornithology (BTO) metal ring together with a
119 unique combination of three colour rings (under BTO licence). Individuals can be sexed
120 according to their wing length because there is minimal overlap between males and females
121 (Demongin 2016); no discrepancies have ever occurred when confirming sex from
122 observations of breeding behaviour (e.g. incubation is carried out solely by females, Tyler &
123 Ormerod 1994). Individuals can be aged as either first years or older ('adults') according to
124 the presence or absence of unmoulted juvenile coverts, respectively (Demongin 2016). All
125 nesting attempts are monitored through to fledging or failure (see below) and every nestling
126 is metal and colour ringed (using the same system as for adults) when between one and two
127 weeks old. Breeding begins in March and the laying of first clutches typically takes place
128 between mid-March and mid-April each year.

129 The rivers and associated streams within the site were surveyed from 15 January to 12
130 February 2016 in order to identify territory holders and floaters. Access restrictions and
131 flooding due to a severe storm in December 2015 meant that only approximately 60% of the
132 site could be reliably surveyed; birds present on the remaining waterways were excluded
133 from the study. Each stretch of river was surveyed once per week and three or four times in
134 total. Surveys involved walking slowly alongside each section of water, identifying all colour
135 ringed birds using binoculars and recording the location where each was first encountered
136 using a Garmin eTrex H GPS unit (Garmin Ltd., Switzerland). Birds were classified as

137 territorial if they were recorded within 500 m of the same location on each survey (typical
138 winter territory sizes in this study population are 500-1000 m in length, SPS unpubl. data; see
139 Results). All of these birds showed behaviour typical of territoriality, including singing,
140 chasing of intruders and consistent ‘double backing’ when pushed in a particular direction
141 (see below). Birds were considered to be in territorial pairs if the same two individuals were
142 recorded together (i.e. within 1-50 m of each other) each time; members of a pair were
143 occasionally found further apart but always reunited when disturbed by the observer or to
144 chase away another bird which had entered their territory. Individuals were classified as
145 floaters if recorded at different locations more than 1 km apart on at least three surveys; these
146 birds were never seen in a pair and did not show any territorial behaviour. All other
147 individuals recorded during the winter survey period were only seen once or twice, in the
148 same or different locations, and were not classified. This included six colour ringed
149 individuals and what we estimate to be a similar number of unmarked birds.

150

151 *Territory size*

152 To measure territory size in the winter and in the breeding season, upstream and downstream
153 territory limits were identified using similar methods to researchers working with other
154 *Cinclus* species (Feck & Hall 2004, Chen & Wang 2010). Birds were gently pushed upstream
155 or downstream by walking behind them until they doubled back in the opposite direction; the
156 turning point was recorded with a GPS. The focal bird was whichever member of a pair the
157 observer first encountered, and visits were abandoned if the focal bird interacted with a
158 conspecific other than its partner (who was rarely more than 15 m away). Two upstream and
159 two downstream limits were identified for each territory, all on separate visits; all pairs of
160 upstream or downstream limits were within 20 m of each other, so no further visits were
161 considered necessary. No territories contained forks in the river or major tributaries. Small

162 tributaries are rarely used by the birds in our study area other than in times of severe flooding,
163 and these streams were therefore excluded from our measurements because it was not
164 possible to push birds onto them. The furthest upstream and downstream limits for each
165 territory were then inputted into ArcGIS version 10.2 (Esri, USA) in order to calculate the
166 length of the territory, measured along the watercourse rather than as the Euclidean distance
167 between the two limits. Winter territories were measured from 15 February to 6 March and,
168 for any given pair, at least four weeks before laying began (median first egg lay date for
169 winter territorial pairs = 2 April, range = 20 March to 12 April); breeding territories were
170 measured between 4 and 29 April after the pair had begun building a nest. It is possible that
171 territory limits may have shifted between the time when winter territories were first identified
172 and when they were measured; however, our observations suggest that the limits remain
173 unchanged until floaters start to pair up and this was not recorded until at least a month after
174 measurements were completed. The breeding territory size of some pairs could not be
175 measured due to access restrictions.

176

177 ***Reproductive success***

178 All nests were found by following birds carrying nest material or by regularly inspecting
179 traditional sites, and then closely monitored until fledging or failure. Once a pair had been
180 observed lining their nest with leaves, the nest was checked every two to three days for eggs
181 in order to determine lay date (i.e. the date on which the first egg of the clutch was laid).
182 Dippers lay one egg per day and do not start incubating until the penultimate or final egg has
183 been laid (Tyler & Ormerod 1994); if fresh eggs are cold it is therefore possible to determine
184 lay date by back calculation. Clutch size was measured approximately one week after
185 incubation had begun by counting the total number of eggs present. After a typical incubation
186 period of 16 days (Tyler & Ormerod 1994), nests were checked daily for hatching; the date of

187 hatching was occasionally missed by up to two days but the nestlings could then be aged
188 from their appearance. All nestlings were ringed and weighed using an electronic balance
189 when they were nine days old. Nests were then checked at least once per week until fledging
190 was due, at which point daily checks were made to confirm fledging and to inspect the nest
191 for dead nestlings. For all successful nests, the number of chicks fledged was taken to be the
192 brood size at ringing as no cases of mortality after this point were recorded.

193

194 *Statistical analysis*

195 The following variables were measured for each nest: lay date, converted into a Julian date as
196 the number of days since the end of February (i.e. 1st March = 1); clutch size; mean nestling
197 mass (the mean body mass of all chicks in the brood when nine days old); and the number of
198 chicks fledged (zero for failed nests). All of these variables and territory sizes were non-
199 normally distributed, so non-parametric tests were used throughout. All analyses were carried
200 out in SPSS version 20 (IBM Corp., USA).

201

202 **Results**

203

204 All birds classified as territorial in winter defended their territories in heterosexual pairs ($n =$
205 14 pairs); six pairs contained at least one first year bird but all 8 pairs comprising two adults
206 had bred together in the previous season (SPS unpubl. data). Most pairs ($9/14 = 64.3\%$) also
207 bred together in the following season. In three of the other pairs, one member was not seen at
208 all after winter and presumed dead, while the remaining member paired up with a bird which
209 had not been recorded at all during winter surveys. The final two pairs switched partners
210 following the breakdown of a bigamous relationship: one female abandoned her part-built
211 nest and the male with which she had defended a winter territory, instead breeding with a bird
212 which had not been classified and leaving her original male to continue breeding with his
213 other female. All floaters ($n = 14$) bred with other floaters or with birds which had either not
214 been classified or not been seen at all during winter ($n = 10$ pairs). There was no clear
215 evidence of any lone birds defending a winter territory, although some of the unclassified
216 birds were occasionally seen chasing other unidentified individuals.

217 The lay dates of pairs which were territorial during winter and remained together ($n =$
218 9) were significantly earlier than those of birds which were territorial but had changed
219 partners since winter ($n = 5$) and those of pairs containing floaters ($n = 10$; Kruskal-Wallis
220 test: $\chi^2 = 11.719$, $df = 2$, $P = 0.003$; Figure 1). The earliest lay date for a winter territorial pair
221 was day 20 (20th March); the earliest lay dates of pairs with new partners or pairs containing
222 floaters were day 41 (10th April) and day 35 (4th April), respectively. By contrast, pairs from
223 the three groups did not differ significantly in their clutch size ($\chi^2 = 0.943$, $df = 2$, $P = 0.624$),
224 mean nestling mass ($\chi^2 = 0.788$, $df = 2$, $P = 0.674$) or number of chicks fledged ($\chi^2 = 1.372$,
225 $df = 2$, $P = 0.504$).

226 For the pairs which remained together throughout the study period, winter territories
227 were significantly shorter than breeding territories (Wilcoxon signed rank test: $Z = 2.666$, $n =$

228 9, $P = 0.008$; Figure 2) but there was a significant positive correlation between the length of
229 winter and breeding territories (Spearman correlation: $r_s = 0.850$, $n = 9$, $P = 0.004$; Figure 3).
230 There was no significant correlation between winter territory length and lay date ($r_s = -0.167$,
231 $n = 9$, $P = 0.667$), clutch size ($r_s = 0.608$, $n = 9$, $P = 0.083$), mean nestling mass ($r_s = 0.095$, n
232 $= 8$, $P = 0.823$) or number of chicks fledged ($r_s = -0.059$, $n = 9$, $P = 0.879$).
233

234 **Discussion**

235

236 Winter territorial behaviour varied between individuals in our study site. This may help to
237 explain the conflicting nature of previous published observations of wintering Dippers; these
238 include reports of highly territorial birds in some regions but an apparent absence of winter
239 territories in others, though in many cases the birds were not individually marked (reviewed
240 in Tyler & Ormerod 1994). All territorial birds remained in heterosexual pairs throughout the
241 winter, many of them established pairs. While it is possible that some of the unclassified
242 birds or those wintering in areas that were not surveyed may have been territorial and single,
243 such birds are unlikely to be common as more than half of the wintering population was
244 classified and solitary birds seen once were, by definition, absent from that location on other
245 visits.

246 Pairs which were territorial in winter and remained together to breed began laying
247 significantly earlier than those comprising birds which had changed partners or pairs
248 containing floaters. This may be selectively advantageous because breeding earlier increases
249 the likelihood that pairs will be able to raise a second brood (Tyler & Ormerod 1985,
250 Ormerod & Tyler 1993, Wilson 1996). Double brooding can substantially increase annual
251 and lifetime reproductive success in birds (e.g. Hoffmann *et al.* 2015, Cornell & Williams
252 2016), although in Dippers these benefits may be offset by lower offspring survival in early
253 and second broods (Ormerod & Tyler 1993). The 2016 breeding season was later than
254 previous seasons (SPS unpubl. data) and only four of the pairs in this study attempted to raise
255 a second brood. It is worth noting that all of these were winter territorial pairs, but further
256 study over multiple seasons is needed to investigate the long-term fitness consequences of
257 winter territoriality.

258 So-called ‘carry-over’ effects have been widely reported in long-distance migrants,
259 with higher quality winter territories enabling individuals to maintain better body condition,
260 arrive on their breeding grounds earlier and have higher reproductive success (Norris *et al.*
261 2004, Paxton & Moore 2015). Similar effects may be operating in Dippers with birds
262 occupying winter territories securing access to good feeding sites, bringing them into
263 breeding condition earlier in the year. If this is the case, then it is perhaps surprising that
264 other reproductive measures did not differ between the groups, although Wilson (1996) also
265 found that earlier breeders raised more second broods yet did not have larger clutches or
266 broods. It may be that the lateness of the 2016 season masked any effects, or that winter
267 territoriality yields fitness benefits not measured here, for example offspring or adult survival.
268 Alternatively, it may simply be that because winter territorial birds had paired up sooner, they
269 began breeding earlier (Zack & Stutchbury 1992). Many had bred together in previous years,
270 and a longer pair bond can also to lead to earlier reproduction (Fowler 1995).

271 Floating may be an alternative winter strategy with fitness benefits we were unable to
272 detect offsetting any costs associated with later reproduction. However, given the greater
273 distances covered by floaters and the high levels of aggression they experience, it seems more
274 likely that these are younger or poorer quality individuals which are unable to compete for
275 winter territories; this is often true of floaters (Smith & Arcese 1989, Sergio *et al.* 2009a)
276 including in other winter territorial species (Stutchbury 1994, Hogstad 1999). Floating may
277 therefore be ‘making the best of a bad situation’, for example by monitoring multiple
278 territories in order to identify vacancies when they arise (Smith 1984, Hogstad 1999). The
279 exact age and body condition of many birds in our study was unknown, but ongoing work
280 will shed more light on the age and quality of floaters relative to territorial birds as well as
281 investigating whether individuals adopt the same strategy in successive winters.

282 Birds that changed partners between winter and the breeding season also laid their
283 clutches later than pairs which remained together throughout. Again, this is likely due to the
284 time spent finding a new partner and the shorter period of pair bonding (Fowler 1995), and
285 there is experimental evidence in other passerines that remaining with the same partner
286 allows pairs to breed sooner (Adkins-Regan & Tomaszycski 2007). Most of the birds in our
287 study changed partner after the disappearance and presumed death of their previous partner.
288 However, it is also possible that some birds 'divorce' to acquire a more compatible or higher
289 quality mate (Choudhury 1995).

290 The smaller size of winter territories than breeding territories held by the same pair is
291 likely a consequence of increases in population density during winter. Birds breeding on
292 upland streams where winter conditions are harsh often move lower to the adjoining rivers
293 and remain there until spring, competing with local territory holders (Tyler & Ormerod
294 1994). Similar findings have been reported in American Dippers *Cinclus mexicanus*, in which
295 altitudinal migration increases winter population densities and reduces the size of available
296 territories (Morrisey *et al.* 2004). However, winter territories may also be shorter than
297 breeding territories because birds spend less time performing energetically expensive
298 behaviour such as flying or territory defence (Bryant *et al.* 1985, Ormerod & Tyler 1991),
299 and make greater use of fish in their diet (Ormerod & Tyler 1991); this may be important at a
300 time when environmental conditions are typically harsher. The finding that pairs with larger
301 winter territories also have larger breeding territories may reflect the quality of these birds
302 and their ability to defend a longer stretch of river while still foraging optimally. Breeding
303 territory quality is often related to individual quality, although it is notoriously challenging to
304 determine the direction of any causal relationship (Germain & Arcese 2014).

305 Sample sizes were small in our study, especially when testing the relationship between
306 territory length and breeding success. Furthermore, it is difficult to assess how the lateness of

307 the 2016 breeding season or the exceptional severity of the storm which preceded the study
308 may have impacted the results. However, it is possible that territory length is a poor measure
309 of territory quality in Dippers. Wilson (1996) found that in areas of deep, slow moving water
310 where food is scarce, Dippers defend longer territories than in wider areas of fast-flowing and
311 well-oxygenated water that provide preferred feeding sites such as riffles. The correlation
312 between winter and breeding territory sizes may simply reflect the number of and distance
313 between riffles in that area; territory length may not predict lay date or breeding success if
314 unrelated to quality. Further work on winter territoriality in this species should therefore
315 include alternative measures of territory quality such as food availability.

316

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318

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324

325 **References**

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424 **Legends to figures**

425

426 **Figure 1.** The mean lay dates (\pm se) of breeding pairs of Dippers with different territorial
427 behaviour in the previous winter. Territorial pairs are divided into those which remained
428 together in the breeding season and those containing birds which changed partners between
429 winter and the breeding season. The remaining pairs are those which contained at least one
430 floater. Letters (a and b) denote significant differences ($P < 0.05$) determined using Dunn-
431 Bonferroni *post hoc* comparisons following a Kruskal-Wallis test.

432

433 **Figure 2.** The mean winter and breeding territory lengths (\pm se) of pairs of Dippers which
434 remained together throughout the study period.

435

436 **Figure 3.** The relationship between winter territory length and breeding territory length in
437 pairs of Dippers which remained together throughout the study period.

438

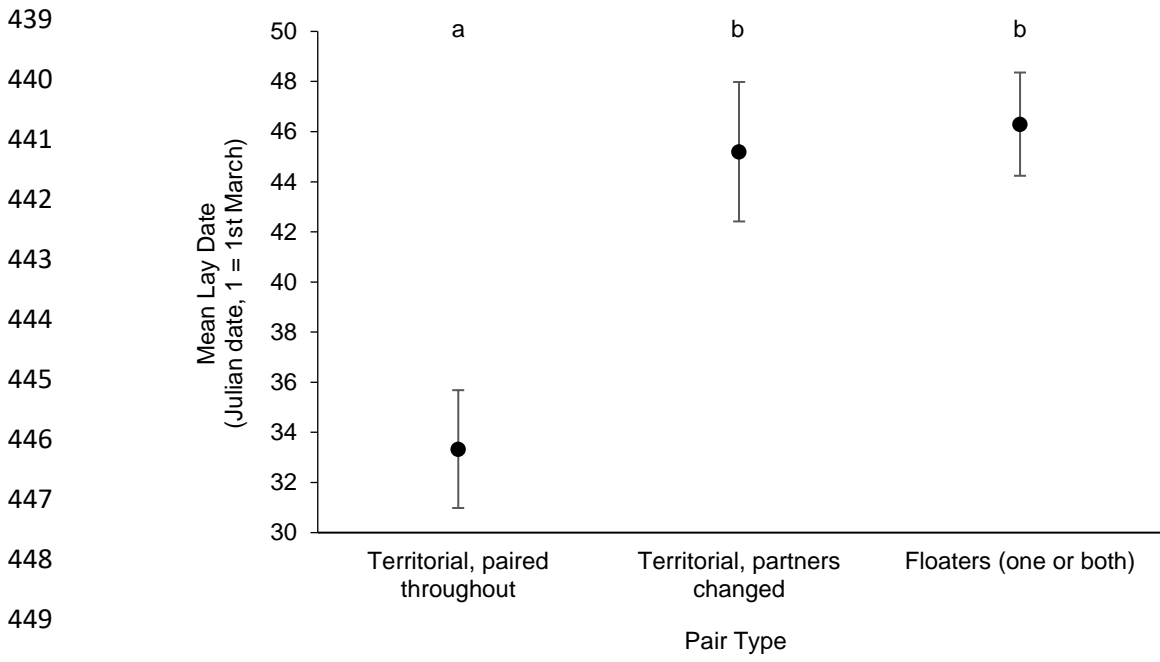


Figure 1

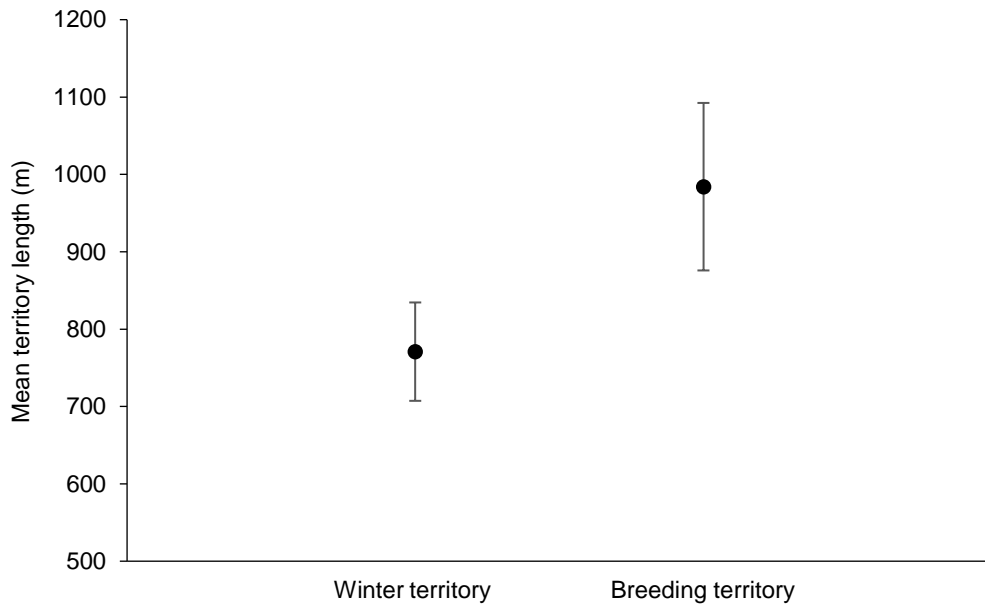
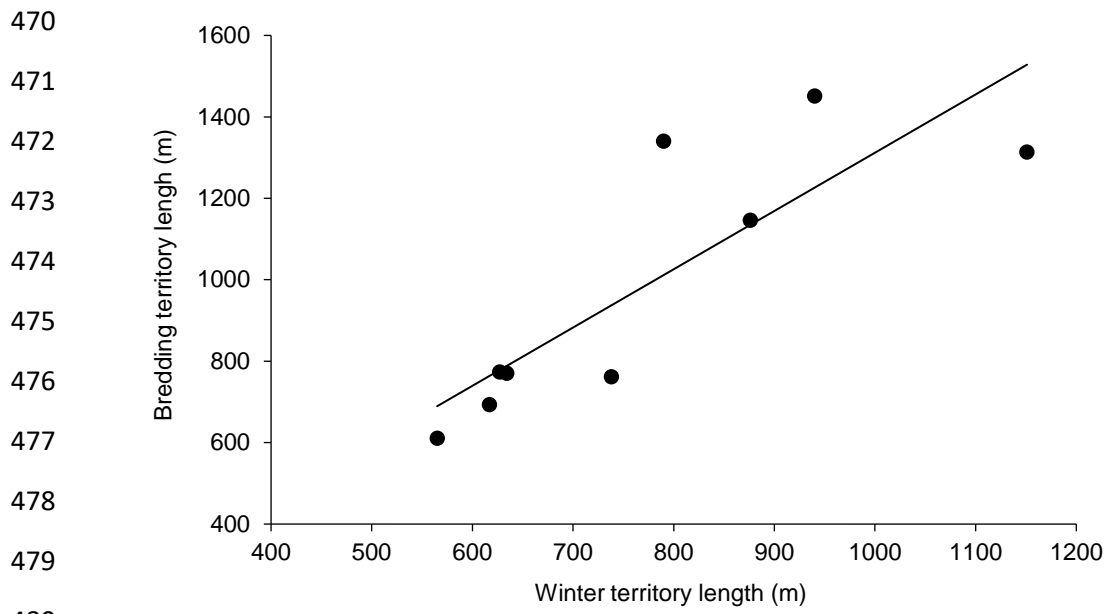


Figure 2



481 **Figure 3**

482