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Aggressive behavioural interactions between swans (*Cygnus* spp.) and other waterbirds during winter: a webcam-based study

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Abstract

Background: Our understanding of any impacts of swans on other waterbirds (including other swans), and potential effects on waterbird community structure, remain limited by a paucity of fundamental behavioural and ecological data, including which species swans interact aggressively with and how frequently such interactions occur.

Methods: Behavioural observations of aggression by swans and other waterbirds in winters 2018/2019 and 2019/2020, were carried out via live-streaming webcams at two wintering sites in the UK. All occurrence sampling was used to identify all aggressive interactions between conspecific or heterospecifics individuals, whilst focal observations were used to record the total time spent by swans on aggressive interactions with other swans. Binomial tests were then used to assess whether the proportion of intraspecific aggressive interactions of each species differed from 0.5 (which would indicate equal numbers of intraspecific and interspecific interactions). Zero-inflated generalized linear mixed effects models (ZIGLMMs) were used to assess between-individual variation in the total time spent by swans on aggressive interactions with other swans.

Results: All three swan species were most frequently aggressive towards, and received most aggression from, their conspecifics. Our 10-min focal observations showed that Whooper (*Cygnus cygnus*) and Bewick's Swans (*C. columbianus bewickii*) spent 13.8 ± 4.7 s (means $\pm$ 95% CI) and 1.4 ± 0.3 s, respectively, on aggression with other swans. These durations were equivalent to 2.3% and 0.2% of the Whooper and Bewick's Swan time-activity budgets, respectively. Model selection indicated that the time spent in aggressive interactions with other swans was best-explained by the number of other swans present for Whooper Swans, and an interactive effect of time of day and winter of observation for Bewick's Swans. However, the relationship between swan numbers and Whooper Swan aggression times was not strong ($R^2 = 19.3\%$).

Conclusions: Whilst swans do exhibit some aggression towards smaller waterbirds, the majority of aggression by swans is directed towards other swans. Aggression focused on conspecifics likely reflects greater overlap in resource use, and hence higher potential for competition, between individuals of the same species. Our study provides an example of how questions relating to avian behaviour can be addressed using methods of remote data collection such as live-streaming webcams.

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Background

Communities of birds that use aquatic habitats (hereafter 'waterbirds') typically contain individuals from multiple species, many of which overlap in terms of the resources that they use (Pöysä 1983; Davis et al. 2014). Such overlaps in resource use can result in aggressive interactions between individuals within waterbird assemblages (Wood et al. 2017; Marchowski and Neubauer 2019). Aggressive behaviours allow individuals to gain and maintain access to valuable limited resources such as food or preferred breeding or resting locations, and to deny other individuals access to those resources (King 1973; Amat 1990; Pelligrini 2008).

Among waterbird assemblages, the true swans (*Cygnus* spp.) are large-bodied, herbivorous waterbirds found on all continents except Antarctica (Rees et al. 2019). Previous authors have highlighted that swans exhibit aggression towards both conspecifics and heterospecifics (Johnsgard 1965). Indeed, there are numerous examples in the literature of aggression by swans towards other waterbirds (e.g. Johnsgard 1965; Tingay 1974; Ely et al. 1987; Burgess and Stickney 1994; Gurtovaya 2000). Swans have been observed to threaten other birds with stylised displays (Lind 1984), and to attack with their bill, wings and body (Johnsgard 1965; Burgess and Stickney 1994), which in some instances has resulted in the death of the targeted individual (e.g. Stone and Marsters 1970; Delacour 1973). For example, Ely et al. (1987) reported that attacks by Whistling Swans (*Cygnus columbianus columbianus*, a subspecies of Tundra Swan) killed two Greater White-fronted Goose (*Anser albifrons*) goslings during the breeding season. Similarly, Brazil (1983) observed a Whooper Swan (*Cygnus cygnus*) attack and kill a juvenile Eurasian Wigeon (*Mareca penelope*) in Iceland. Despite such reports, recent studies have pointed out that the extent of aggressive behaviours by swans, and the possible impacts that these may have on other waterbirds, are poorly understood (Gayet et al. 2011; Wood et al. 2019a). Moreover, two studies of breeding waterbirds found no evidence that swans exclude other waterbirds from habitat or reduce breeding densities (Gayet et al. 2011, 2016). A recent meta-analysis cast further doubt, by showing that swans spent no more time engaged in aggressive behavioural interactions than other waterbird taxa (Wood et al. 2017).

Nevertheless, aggression by swans towards other waterbirds continues to be relevant for the management and conservation of waterbirds and their habitats. In North America, there have been attempts to eradicate an invasive population of Mute Swans (*Cygnus olor*) due to concerns about the effects of swans on native species, including other waterbirds. For example, in Maryland, USA, a newly established Mute Swan moulting flock displaced a mixed breeding colony of Least Tern (*Sterna antillarum*) and Black Skimmer (*Rynchops niger*), two species of local conservation concern (Therres and Brinkler 2004). Waterbird managers and conservationists have also expressed concerns that the invasive Mute Swans could out-compete the native Trumpeter (*Cygnus buccinator*) or Whistling Swans for food and habitat (Lumsden 2016). Similarly, conservationists have questioned whether the observed c. 39% decline in winter Bewick's Swan (*C. columbianus bewickii*) numbers in north-west Europe between 1995 and 2010 may be at least partially attributable to competition with rising numbers of Whooper and Mute Swans in the region (Rees et al. 2019). Even among conspecifics, interference competition among foraging swans can reduce food intake rates (Gyimesi et al. 2010). In the Russian Arctic, concerns of local hunters regarding the impacts of swans on other waterbirds have been identified as a motivation for the illegal persecution of Bewick's Swans (Newth et al. in press). Similarly, legal hunting of Whistling Swans in parts of the USA has been justified on the basis that competition between the swans and other waterbirds has been deemed excessive (Sladen 1991). However, our understanding of any impacts of swans on other waterbirds (including other swans), and potential effects on waterbird community structure, remain limited by a paucity of fundamental behavioural and ecological data, including which species swans interact aggressively with and how frequently such interactions occur.

In this study we used repeated behavioural observations at two wintering sites to improve our understanding of which species swans interact aggressively with and how frequently such interactions occur. We used the behavioural data that we obtained to test three hypotheses. As Peiman and Robinson (2010) reported that aggression is more likely between individuals with the greatest overlap in resource use, our first hypothesis (hereafter termed the '*conspecific hypothesis*') was that swans would devote more time to intraspecific aggression compared with interspecific aggression. Aggressive behaviours among birds typically become more common as the density of individuals within a habitat increases (Metcalfe and Furness 1987;

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Wood et al. 2015), thus our second hypothesis (hereafter termed the '*density hypothesis*') was that swans would spend more time engaged in aggressive interactions when present in higher density flocks. Finally, we expected that as winter progressed, a dominance hierarchy would establish among individual swans within their flock, and so reduce further aggression; indeed, Scott (1981) reported that the frequency of fights between Bewick's Swans declined progressively over winter months. Therefore, our third hypothesis (hereafter termed the '*winter decline hypothesis*') was that swans would spend more time engaged in aggressive interactions in early winter months compared with later months.

Methods

Study systems

Our study focused on two wetlands used by wintering waterbirds in the UK; the Wildfowl & Wetland Trust (WWT) Centre reserves at Slimbridge (51°44′29.3″ N, 2°24′21.52″ W) and Caerlaverock (54°59′2.4″ N, 3°30′0″ W), in southwest England and southwest Scotland, respectively. Both wetland sites feature a mosaic of aquatic and terrestrial habitats, most notably small lakes used by waterbirds for feeding and roosting. In recent winters Slimbridge has supported both Bewick's Swans and Mute Swans, whilst Caerlaverock has supported Mute and Whooper Swans (Black and Rees 1984). The mean of the peak winter counts of individual swans between 2014/2015 and 2018/2019 was 149 Bewick's Swans (range 116–212) and 441 Mute Swans (range 374–500) in the Severn Estuary (which includes Slimbridge), and 337 Whooper (range 257–487) and 74 Mute Swans (range 70–83) in the Solway Estuary (which includes Caerlaverock) (Frost et al. 2020). Swans at both sites share feeding and roosting habitat with a range of smaller-bodied waterbird species, including geese such as Canada Geese (*Branta canadensis*) and Greylag Geese (*Anser anser*), dabbling ducks such as Northern Mallard (*Anas platyrhynchos*), Eurasian Teal (*Anas crecca*), and Northern Pintail (*Anas acuta*), diving ducks such as Tufted Duck (*Aythya fuligula*) and Common Pochard (*Aythya ferina*), Rallidae such as Eurasian Coot (*Fulica atra*) and Common Moorhen (*Gallinula chloropus*), as well as Common Shelduck (*Tadorna tadorna*), and gull species (*Larus* spp.). The non-migratory Mute Swans are resident at both Slimbridge and Caerlaverock throughout the year, and Bewick's Swans are typically present at Slimbridge between November and February, whilst Whooper Swans use Caerlaverock between October and March (Black and Rees 1984; Rees 2006).

Data collection

We used two ways of collecting data concurrently from observations made during periods of one hour in duration: one way was used to record aggression between any two individuals of any waterbird species to address our *conspecific hypothesis*, and the second way was used to record swan-specific aggression to address our *density* and *winter decline hypotheses*. First we used all occurrence sampling to record all incidents of aggression between individuals over the course of the hour-long observation period (Altmann 1974), based on an ethogram of the aggressive behaviours observed during preliminary observations at both sites in October 2018. These preliminary observations indicated a number of aggressive behaviours consistent with previous work (Johnsgard 1965), including strikes made with the bill, wings, or body, as well as chasing and lunging at another individual. For each aggressive behaviour that was observed, the species identities of both the aggressor and its opponent were recorded; all species were identified on the basis of size, body shape, and plumage characteristics, with the aid of an online photo-identification guide (RSPB 2018).

To address our *density* and *winter decline hypotheses* regarding the variations in aggression with swan numbers and between months, we used focal sampling (Altmann 1974) to quantify the total time that Bewick's and Whooper Swans spent engaged in aggressive interactions with other swans. During each hour-long observation period, an observer selected a swan at random and used a stopwatch to record the duration of each aggressive interaction with another swan in a 10-min observation period; hence, six individual swans could be observed during each hour-long observation. A focal observation duration of 10 min was selected in order to make our study comparable with earlier time-activity budget of swans that used an observation duration of 10 min (e.g. O'Hare et al. 2007; Tatu et al. 2007; Wood et al. 2019b). Both immediately before and after each hour-long observation period, the number of swans that could be observed was counted, with the mean average taken as the number of swans present during that observation.

All behavioural data were collected remotely via livestreaming webcams (AXIS Q6035-E PTZ Dome Network Camera), which were fixed in place at both sites. Both webcams faced directly outwards over the study lake from the shore, and each webcam maintained the same zoom so that the field-of-view was standardised across all observation periods (Additional file 1: Figure S1). As our study was conducted entirely via the webcams, we do not know the precise numbers of birds outside of the cameras field-of-view, but we suspect it to be low as the cameras covered major proportions of the surface area

of each lake (Additional file 1: Figure S1). Webcams have been shown previously to be useful tools in behavioural studies, which allow remote collection of data with limited disturbance to the focal birds (e.g. Anderson et al. 2011; Schulwitz et al. 2018). During winter months in 2018/2019 (November 2018–February 2019, inclusive) and 2019/2020 (November 2019–December 2019, inclusive), webcam footage from WWT Slimbridge was watched for 1 h on an average of 7.5 days per month at either 08:30 a.m. to 09:30 a.m. (hereafter "AM"), 11:30 a.m. to 12:30 p.m. (hereafter "MID") or 14:30 p.m. to 15:30 p.m. (hereafter "PM"); these times were selected to achieve a balanced study design and to avoid coinciding with the periods when food (wheat grains) is provided as part of a public engagement programme. Winter storms at the start of January 2020 regrettably damaged the webcam and prevented further data collection. We aimed to use the same methodology for WWT Caerlaverock, however, the webcam suffered a technical failure after data for only November 2018 could be collected. Similar technical issues precluded data collection at WWT Caerlaverock during winter 2019/2020. Our sampling methodology of ten observations per hour, on an average of 7.5 days per month, over 6 months, yielded a total of 450 observations at Slimbridge; however, swans were only present during 282 of these. In contrast, swans were present at Caerlaverock during every observation period. In total, we therefore obtained 282 focal observations (of 10 min each) from WWT Slimbridge and 42 focal observations (of 10 min each) from WWT Caerlaverock. While we cannot discount the possibility that some individuals were observed on multiple occasions, the aforementioned large numbers of individual swans present at both sites mean that this is unlikely to have been a major issue.

Statistical analyses

All statistical analyses were carried out using R version 3.6.3 (R Core Team 2020). To address our *conspecific hypothesis* that intraspecific interactions would be observed more frequently than interspecific interactions, we used two-tailed binomial tests to assess the statistical significance of the deviation of the proportion of intraspecific aggressive interactions of each species from 0.5 (which would indicate equal numbers of intraspecific and interspecific interactions). For each of our focal species, separate tests were carried out for aggressive interactions (i) targeted at other individuals, and (ii) received from other individuals. Statistically significant differences between proportions were attributed where $P < 0.05$, after P values had been adjusted using Holm-Bonferroni corrections to account for multiple comparisons (Holm 1979). Our binomial tests also allowed 95% confidence

intervals to be estimated for the proportions of intraspecific and interspecific interactions (Clopper and Pearson 1934). In addition, we used two-sample binomial tests for equality of proportions to assess the significance of the differences between species in their proportion of interspecific aggressive interactions recorded towards other birds; P values were again adjusted using Holm-Bonferroni corrections (Holm 1979).

To address our *density* and *winter decline hypotheses* regarding the variations in aggression with swan numbers and between months, we used zero-inflated generalized linear mixed effects models (ZIGLMMs), using the glmmTMB R package (Brooks et al. 2017). Zero-inflated models were required because of the relatively high proportions of zeros in the data sets (i.e. observations during which no aggression was recorded). In each model, our response variable was the number of seconds spent in aggressive interactions by each individual recorded during our focal observation. As the aforementioned issues with the webcam at WWT Caerlaverock prevented data collection after November 2018, the resulting datasets for Bewick's and Whooper Swans were markedly different in terms of the sample size and the temporal replication. Therefore, we analysed the data for Whooper and Bewick's Swans separately. For each species, we ran and compared candidate models that comprised all possible combinations of additive and two-way interactions between our explanatory variables, as well as the null model. For Whooper Swans, we considered the following explanatory variables: (i) the time of day of the observation, a categorical factor with three levels (AM, MID, and PM), and (ii) the mean number of swans present during the observation. For Bewick's Swans we considered the following explanatory variables: (i) the time of day of the observation, a categorical factor with three levels (AM, MID, and PM), (ii) the mean number of swans present during the observation, (iii) the month of observation, a categorical factor with four levels (November, December, January, and February), and (iv) the winter of observation, a categorical factor with two levels ("A" = 2018/2019 and "B" = 2019/2020). In addition, a categorical variable unique to each observation block (termed the 'observation identity'), was fitted as a random intercept in each model to account for the non-independence of individual swans observed within the same hour-long observation period. Preliminary comparisons of global models using second-order Akaike's Information Criteria (AIC$_c$; Burnham et al. 2011) showed that for the zero-inflated generalized linear mixed effects models of the Whooper Swan data, a negative binomial distribution in which the variance increased linearly with the mean (Brooks et al. 2017) performed better than either a negative binomial distribution in which the variance increased quadratically

with the mean ($\Delta AIC_c = 4.31$), or a Poisson distribution ($\Delta AIC_c = 169.40$). For Bewick's Swans there was little difference between models with either of the two negative binomial distributions ($\Delta AIC_c = 0.24$), whilst the Poisson distribution did not converge. Therefore, in all subsequent models we used the negative binomial distribution in which the variance increased linearly with the mean.

To ensure that collinearity did not confound our modelling (Dormann et al. 2013), we tested for covariance among our explanatory variables. To our knowledge, Variance Inflation Factors (VIFs), which are typically used to identify collinear variables in linear models (Dormann et al. 2013), are not currently available for ZIGLMMs, and so alternative methods were used. One-way Analysis of Variance (ANOVA) was used to test for covariance between our continuous variable (number of swans present) and each of our categorical variables: time of day, month, and winter. Significant covariance was inferred where statistically significant differences in the mean number of swans present per categorical variable level were detected. Values for the number of swans present were square-root transformed so that model residuals satisfied the assumptions of the ANOVA tests (Zuur et al. 2010). Associations between the frequencies of pairs of categorical variables were tested using χ^2 tests where all frequencies were ≥ 5, or Fisher's exact test where one or more frequencies were < 5 (Crawley 2013). Significant covariance between variables was inferred where statistically significant associations between the variables were found. Using these methods, we found for Whooper Swans a significant effect of time of day on the number of swans present (ANOVA: $F_{2,39} = 47.27$, $P < 0.001$). For Bewick's Swans we detected covariance between the number of swans present and both the time of day (ANOVA: $F_{2,279} = 12.24$, $P < 0.001$) and winter (ANOVA: $F_{1,280} = 22.81$, $P < 0.001$), as well as between winter and month (Fisher's exact test: $P < 0.001$); all other tests were non-significant ($P > 0.05$). Consequently, these collinear variables were not permitted within the same candidate models. Therefore, in total we ran 3 and 11 candidate models for the Whooper Swan and Bewick's Swan datasets, respectively, accounting for all possible non-collinear combinations of additive and two-way interactions between our explanatory variables.

We compared the relative support of each candidate model using AIC_c, calculated using the MuMIn R package (Barton 2019). Typically the model with the lowest AIC_c value is considered to be the best-supported by the data, but we also considered models to be competitive where AIC_c values < 6.0, following the advice of Richards (2008) for dealing with overdispersion. Furthermore, to avoid selecting models with uninformative parameters, we considered that a

model with one additional parameter was competitive only if the associated AIC_c value was lower than the more parsimonious model (Arnold 2010). Three further metrics for each model were used as indicators of the relative strength of support in the data, to facilitate more detailed comparisons among our candidate models: (i) the probability of a model being the best-fitting model compared with the best-supported model shown by AIC_c (Relative Likelihood *RL*), (ii) the ratio of ΔAIC_c values for each model relative to the whole set of candidate models (Akaike weight w_i), and (iii) how many more times less likely a model is to be the best-fitting model compared with the best-supported model shown by AIC_c (Evidence Ratio *ER*) (Burnham et al. 2011). In addition, to quantify the explanatory power of each model (Mac Nally et al. 2018), the conditional and marginal R^2 values, which represented the proportion of the between-swan variance in the time spent on aggression that was accounted for both the fixed and random effects combined and the fixed effects alone, respectively (Nakagawa et al. 2017), were calculated for each model using the sjstats R package (Lüdecke 2020). Finally, Tukey's post hoc comparisons of the estimated marginal means of variables within our best-supported models were carried out using the emmeans R package (Lenth 2020).

Results

Intraspecific versus interspecific aggression

For 13 out of 14 focal waterbird species, the majority of aggressive behavioural interactions were given by, and received from, conspecifics (Table 1). Overall, we observed aggression by the three swan species towards 9 of the 11 smaller waterbird species, whilst in turn the swans received aggression from 8 of the 11 species (Table 1).

The proportion of aggressive interactions directed by swans towards conspecifics ranged from 0.589 (95% CI 0.540–0.637) among Bewick's Swans to 0.801 (0.733–0.858) among Whooper Swans (Table 2; Fig. 1). Similarly, the proportion of aggressive interactions received by swans from their conspecifics ranged from 0.623 (0.555–0.687) for Whooper Swans up to 0.912 (0.880–0.938) among Mute Swans (Table 2; Fig. 1). For both the interactions directed towards, and received from, conspecifics, the proportions of aggressive interactions that were intraspecific were significantly greater for all three swan species ($P \leq 0.003$ in all cases); i.e. intraspecific interactions were more frequent than interspecific interactions (Table 2; Fig. 1). Among the 11 species of smaller waterbirds, intraspecific interactions directed towards other individuals were significantly more frequent in 8 species,

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Table 1 The total numbers of aggressive interactions (*n*) given and received by each focal waterbird species

Focal species	Aggression towards	*n*	Aggression from	*n*
Bewick's Swan	Bewick's Swan	245	Bewick's Swan	245
	Northern Pintail	37	Northern Pintail	11
	Tufted Duck	32	Tufted Duck	3
	Eurasian Coot	30	Eurasian Coot	4
	Canada Goose	19	Canada Goose	16
	Eurasian Teal	17	Eurasian Teal	1
	Northern Mallard	11	Northern Mallard	2
	Common Moorhen	9	Common Moorhen	1
	Gull spp.	9	Gull spp.	0
	Greylag Goose	7	Greylag Goose	7
	Mute Swan	0	Mute Swan	23
Mute Swan	Mute Swan	364	Mute Swan	364
	Whooper Swan	80	Whooper Swan	27
	Northern Mallard	31	Northern Mallard	3
	Bewick's Swan	23	Bewick's Swan	0
	Canada Goose	19	Canada Goose	5
	Northern Pintail	1	Northern Pintail	0
	Gull spp.	1	Gull spp.	0
Whooper Swan	Whooper Swan	137	Whooper Swan	137
	Mute Swan	27	Mute Swan	80
	Northern Mallard	7	Northern Mallard	1
	Canada Goose	0	Canada Goose	2
Canada Goose	Canada Goose	190	Canada Goose	190
	Northern Mallard	28	Northern Mallard	3
	Bewick's Swan	16	Bewick's Swan	19
	Mute Swan	5	Mute Swan	19
	Northern Pintail	2	Northern Pintail	1
	Whooper Swan	2	Whooper Swan	0
	Tufted Duck	1	Tufted Duck	0
	Eurasian Teal	1	Eurasian Teal	0
	Greylag Goose	0	Greylag Goose	3
Greylag Goose	Greylag Goose	39	Greylag Goose	39
	Bewick's Swan	7	Bewick's Swan	7
	Canada Goose	3	Canada Goose	0
	Northern Mallard	2	Northern Mallard	0
	Northern Pintail	2	Northern Pintail	0
	Tufted Duck	1	Tufted Duck	0
Common Shelduck	Common Shelduck	2	Common Shelduck	2
	Eurasian Coot	3	Eurasian Coot	0
Northern Mallard	Northern Mallard	240	Northern Mallard	240
	Northern Pintail	56	Northern Pintail	26
	Tufted Duck	9	Tufted Duck	23
	Eurasian Coot	7	Eurasian Coot	1
	Eurasian Teal	6	Eurasian Teal	4
	Common Moorhen	6	Common Moorhen	3
	Canada Goose	4	Canada Goose	28

Table 1 (continued)

Focal species	Aggression towards	*n*	Aggression from	*n*
	Mute Swan	3	Mute Swan	31
	Bewick's Swan	2	Bewick's Swan	11
	Whooper Swan	1	Whooper Swan	7
	Common Pochard	1	Common Pochard	0
	Gull spp.	1	Gull spp.	0
	Greylag Goose	0	Greylag Goose	2
Northern Pintail	Northern Pintail	356	Northern Pintail	356
	Eurasian Teal	38	Eurasian Teal	24
	Northern Mallard	26	Northern Mallard	56
	Common Moorhen	22	Common Moorhen	18
	Bewick's Swan	11	Bewick's Swan	37
	Eurasian Coot	8	Eurasian Coot	21
	Tufted Duck	4	Tufted Duck	10
	Canada Goose	1	Canada Goose	2
	Mute Swan	0	Mute Swan	1
	Greylag Goose	0	Greylag Goose	2
Eurasian Teal	Eurasian Teal	146	Eurasian Teal	146
	Northern Pintail	24	Northern Pintail	38
	Eurasian Coot	10	Eurasian Coot	12
	Northern Mallard	4	Northern Mallard	6
	Bewick's Swan	1	Bewick's Swan	17
	Canada Goose	0	Canada Goose	1
Tufted Duck	Tufted Duck	152	Tufted Duck	152
	Northern Mallard	23	Northern Mallard	9
	Northern Pintail	10	Northern Pintail	4
	Bewick's Swan	3	Bewick's Swan	32
	Eurasian Coot	3	Eurasian Coot	1
	Common Pochard	1	Common Pochard	3
	Canada Goose	0	Canada Goose	1
	Greylag Goose	0	Greylag Goose	1
Common Pochard	Common Pochard	10	Common Pochard	10
	Tufted Duck	3	Tufted Duck	1
	Eurasian Coot	2	Eurasian Coot	0
	Northern Mallard	0	Northern Mallard	1
Eurasian Coot	Eurasian Coot	61	Eurasian Coot	61
	Northern Pintail	20	Northern Pintail	8
	Eurasian Teal	12	Eurasian Teal	10
	Common Moorhen	4	Common Moorhen	3
	Bewick's Swan	3	Bewick's Swan	30
	Northern Mallard	1	Northern Mallard	7
	Tufted Duck	0	Tufted Duck	3
	Common Pochard	0	Common Pochard	2
	Common Shelduck	0	Common Shelduck	3
Common Moorhen	Common Moorhen	102	Common Moorhen	102
	Northern Pintail	18	Northern Pintail	22
	Northern Mallard	3	Northern Mallard	6

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Table 1 (continued)

Focal species	Aggression towards	n	Aggression from	n
	Eurasian Coot	3	Eurasian Coot	4
	Bewick's Swan	1	Bewick's Swan	9
Gull spp.	Gull spp.	19	Gull spp.	19
	Bewick's Swan	0	Bewick's Swan	9
	Mute Swan	0	Mute Swan	1
	Northern Mallard	0	Northern Mallard	1

whilst intraspecific interactions received from other individuals were significantly more frequent in 7 species (Table 2; Fig. 1).

Species comparisons of interspecific aggression

The proportion of interspecific aggressive interactions towards other birds was significantly greater in Bewick's Swans (mean = 0.411, 95% CI 0.363–0.460) than in Mute Swans, Whooper Swans, Canada Geese, Northern Mallard, Northern Pintail, Eurasian Teal, Tufted Duck, and Common Moorhen (Table 3). The difference in the proportions of interspecific aggression towards other species in Whooper Swans (mean = 0.199, 95% CI 0.142–0.267) and Eurasian Coots (mean = 0.396, 95% CI 0.300–0.498) was close to significance, with an adjusted P value of 0.058. No other differences between species were found to be statistically significant (Table 3).

Swan aggression times

Whooper Swans at WWT Caerlaverock spent a mean (± 95% CI) of 13.8 ± 4.7 s engaged in aggressive interactions with other swans, based on the sample of 42 focal observations collected during November 2018; this duration was equivalent to 2.3 ± 0.8% of their time-activity

Table 2 The intra- and interspecific aggressive interactions given and received by each focal waterbird species

Species	Interaction	n_{Intra}	n_{Inter}	n_{Total}	P_{Intra}	P_{Intra} 95% CI	P_{Inter}	P_{Inter} 95% CI	P value
Bewick's Swan	To other	245	171	416	0.589	0.540–0.637	0.411	0.363–0.460	0.003
	From other	245	68	313	0.783	0.733–0.827	0.217	0.173–0.267	< 0.001
Mute Swan	To other	364	155	519	0.701	0.660–0.740	0.299	0.260–0.340	< 0.001
	From other	364	35	399	0.912	0.880–0.938	0.088	0.062–0.120	< 0.001
Whooper Swan	To other	137	34	171	0.801	0.733–0.858	0.199	0.142–0.267	< 0.001
	From other	137	83	220	0.623	0.555–0.687	0.377	0.313–0.445	0.003
Canada Goose	To other	190	55	245	0.776	0.718–0.826	0.224	0.174–0.282	< 0.001
	From other	190	45	235	0.809	0.752–0.857	0.191	0.143–0.248	< 0.001
Greylag Goose	To other	39	15	54	0.722	0.584–0.835	0.278	0.165–0.416	0.012
	From other	39	7	46	0.848	0.711–0.937	0.152	0.063–0.289	< 0.001
Common Shelduck	To other	2	3	5	0.400	0.053–0.853	0.600	0.147–0.947	1.000
	From other	2	0	2	1.000	0.158–1.000	0.000	0.000–0.842	1.000
Northern Mallard	To other	240	96	336	0.714	0.663–0.762	0.286	0.238–0.337	< 0.001
	From other	240	136	376	0.638	0.587–0.687	0.362	0.313–0.413	< 0.001
Northern Pintail	To other	356	110	466	0.764	0.723–0.802	0.236	0.198–0.277	< 0.001
	From other	356	171	527	0.676	0.634–0.715	0.324	0.285–0.366	< 0.001
Eurasian Teal	To other	146	39	185	0.789	0.723–0.846	0.211	0.154–0.277	< 0.001
	From other	146	74	220	0.664	0.597–0.726	0.336	0.274–0.403	< 0.001
Tufted Duck	To other	152	40	192	0.792	0.727–0.847	0.208	0.153–0.273	< 0.001
	From other	152	51	203	0.749	0.683–0.807	0.251	0.193–0.317	< 0.001
Common Pochard	To other	10	5	15	0.667	0.384–0.882	0.333	0.118–0.616	1.000
	From other	10	2	12	0.833	0.516–0.979	0.167	0.021–0.484	0.270
Eurasian Coot	To other	61	40	101	0.604	0.502–0.700	0.396	0.300–0.498	0.276
	From other	61	66	127	0.480	0.391–0.571	0.520	0.429–0.609	1.000
Common Moorhen	To other	102	25	127	0.803	0.723–0.868	0.197	0.132–0.277	< 0.001
	From other	102	41	143	0.713	0.632–0.786	0.287	0.214–0.368	< 0.001
Gull spp.	To other	19	0	19	1.000	0.824–1.000	0.000	0.000–0.176	< 0.001
	From other	19	11	30	0.633	0.439–0.801	0.367	0.199–0.561	1.000

A comparison of the proportions of intraspecific (P_{Intra}) and interspecific (P_{Inter}) aggressive interactions given and received by each focal waterbird species. All P values associated with our binomial tests were adjusted using Holm-Bonferroni corrections for multiple comparisons. Total numbers of interactions (n) are also indicated

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(See figure on next page.)
Fig. 1 The proportions of intraspecific and interspecific aggressive interactions, directed towards or received from, other individuals. Error bars represent the ± 95% binomial CIs. Common Shelduck and Gull spp. are not shown due to low sample sizes. Statistical significance of differences between intraspecific and interspecific proportions is shown in Table 2

budget. A comparison of candidate models showed that the time spent by individual Whooper Swans in aggressive interactions with other swans was best explained by the mean number of swans present during the observation (Table 4). This model had the lowest AIC_c value and accounted for approximately 51% of the total Akaike weights (Table 4). In this model, the time spent in aggressive interactions by Whooper Swans increased with the mean number of swans present (Table 5; Fig. 2). Overall, the effect of swan numbers together with the random effect accounted for 35.1% of the variance in swan aggression times in total, with the effect of swan numbers accounting for 19.3% of the variance. However, two other models had associated AIC_c values within our threshold of 6.0 of this best-supported model. The null model, comprised of only an intercept and random effect term, had a ΔAIC_c value of 0.45 and accounted for c. 40% of the total Akaike weights (Table 4). As the model containing the effect of swan numbers performed only marginally better than the null model, this suggests that the effect of swan numbers was not strong and had limited explanatory power, and hence an effect of swan numbers should be interpreted cautiously. Finally, a model in which aggression time varied with the time of day of the observation had an associated ΔAIC_c value of 3.42; however, the overall support for this model was weak, as it accounted for only c. 9% of the total Akaike weights and the evidence ratio value indicated that it was > 5.5 times less likely to be best-fitting model compared with the lowest AIC_c model (Table 4). Moreover, the model containing time of day performed less well than the null model (Table 4), and so overall we considered that there was little evidence that Whooper Swan aggression time varied among the three times of day (Fig. 3).

Bewick's Swans at WWT Slimbridge spent a mean (± 95% CI) of 1.4 ± 0.3 s engaged in aggressive interactions with other swans, based on the sample of 282 focal observations collected during winters 2018/2019 and 2019/2020; this duration was equivalent to 0.2 ± 0.1% of their time-activity budget. Comparison of our candidate models revealed that the time spent by individual Bewick's Swans in aggressive interactions with other swans was best explained by an interaction between the time of day and the winter of observation (Tables 4, 5). Post-hoc testing indicated that swan aggression times varied between time of day and the winter of observation such that swans spent less time on aggression

during observations made during the afternoons in winter 2019/2020 than during either the afternoons of winter 2018/2019 or midday observations in winter 2019/2020 (Table 6; Fig. 3); no other comparisons were significantly different. This model had the lowest AIC_c value and accounted for > 66% of the total Akaike weights (Table 4). Overall, the effects of time of day and winter together with the random effect accounted for 34.3% of the variance in swan aggression times in total, with the effect of time of day and winter accounting for 23.3% of the variance (Table 4). Crucially, this best-supported model had a lower AIC_c value than the null model ($\Delta AIC_c = 3.24$; Table 4). A further three candidate models also had ΔAIC_c values within our threshold of 6.0 of the minimum AIC_c value, although none of these performed better than the null model (Table 4). Two of these three models comprised the single additive effects contained within our best-supported model, time of day ($\Delta AIC_c = 5.94$) and winter ($\Delta AIC_c = 5.31$). The third comprised the numbers of swans present during the observation ($\Delta AIC_c = 4.74$), but the support for this model was weak. The model of the numbers of swans accounted for only c. 6% of the total Akaike weights and the evidence ratio value indicated that it was > 10.68 times less likely to be best-fitting model compared with the lowest AIC_c model (Table 4). As a fixed effect the number of swans accounted for only 0.7% of the variance in the time spent in aggressive interactions (Table 4; Fig. 2), and so overall we considered that there was little evidence that the numbers of swans present had an effect on the time spent on aggression by Bewick's Swans.

Discussion

In accordance with our *conspecific hypothesis*, we found that aggressive interactions by swans were typically directed towards other swans rather than smaller waterbirds. Indeed, across all three swan species intraspecific aggression accounted for between 59 and 80% of all aggressive interactions directed at other individuals. Previous studies of Mute Swans by Conover and Kania (1994) and Włodarczyk and Minias (2015) found similarly that 47% and 80%, respectively, of all aggressive behaviours were directed towards conspecifics. Our data showed that all three swan species received the greatest proportion of interspecific aggression from another swan
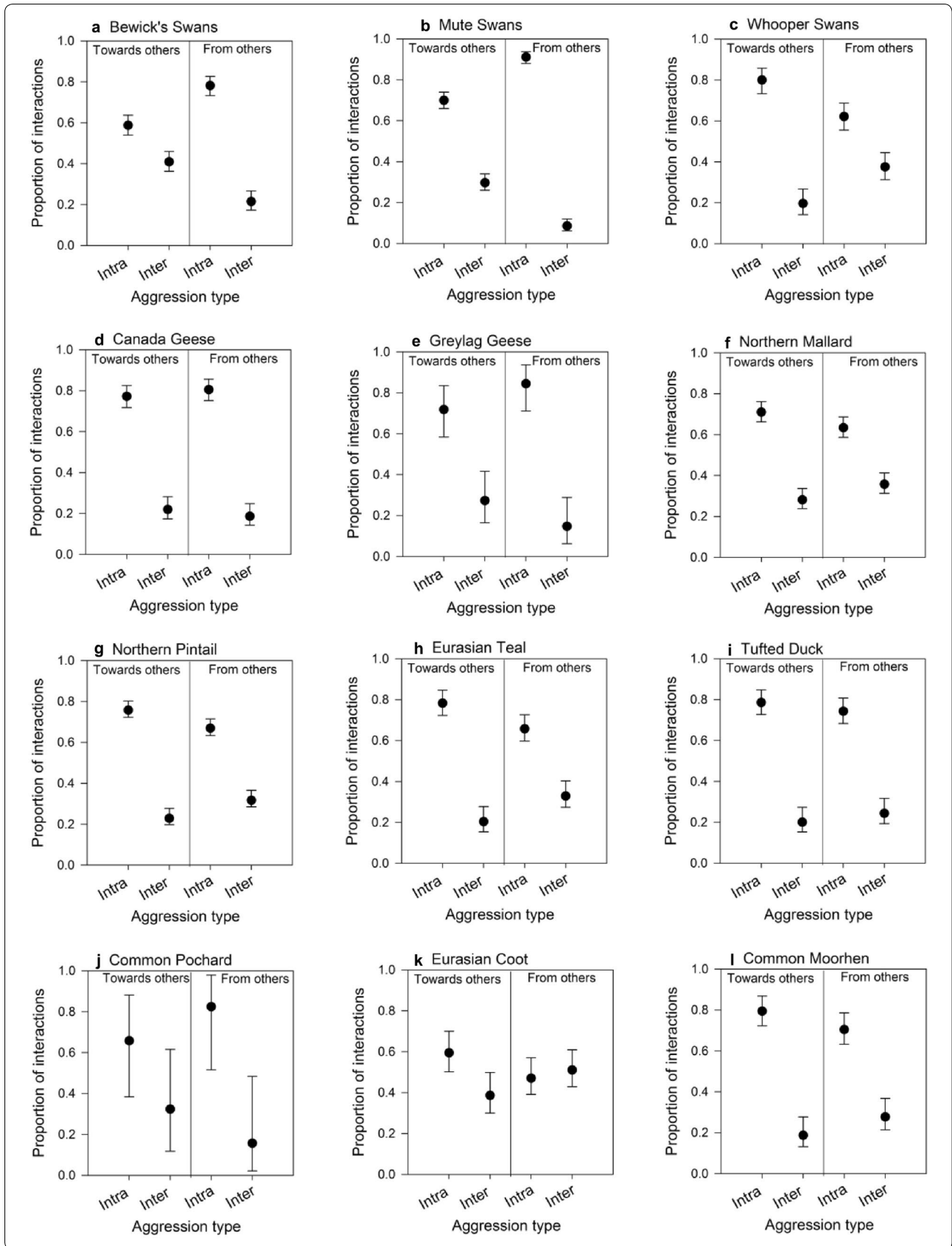
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Table 3 Statistical comparison of the proportion of aggressive interactions that were interspecific

	Bewick's Swan	Mute Swan	Whooper Swan	Canada Goose	Greylag Goose	Common Shelduck	Northern Mallard	Northern Pintail	Eurasian Teal	Tufted Duck	Common Pochard	Eurasian Coot	Common Moorhen	Gull spp.
Bewick's Swan	–	0.037	0.000	0.000	1.000	1.000	0.040	0.000	0.000	0.000	1.000	1.000	0.002	0.067
Mute Swan	12.36	–	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.763
Whooper Swan	23.09	5.95	–	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.058	1.000	1.000
Canada Goose	23.03	4.23	0.26	–	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.140	1.000	1.000
Greylag Goose	3.02	0.03	1.07	0.44	–	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
Common Shelduck	0.16	0.94	2.60	2.06	0.98	–	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.328
Northern Mallard	12.21	0.11	4.04	2.45	<0.01	1.08	–	1.000	1.000	1.000	1.000	1.000	1.000	1.000
Northern Pintail	30.21	4.58	0.79	0.06	0.26	1.87	2.27	–	1.000	1.000	1.000	1.000	1.000	1.000
Eurasian Teal	21.72	4.84	0.02	0.05	0.72	2.32	3.11	0.35	–	1.000	1.000	0.106	1.000	1.000
Tufted Duck	22.94	5.30	0.01	0.08	0.80	2.39	3.43	0.45	<0.01	–	1.000	0.081	1.000	1.000
Common Pochard	0.11	<0.01	0.80	0.43	0.01	0.28	0.01	0.32	0.60	0.65	–	1.000	1.000	1.000
Eurasian Coot	0.03	3.28	11.49	9.72	1.66	0.19	3.91	10.11	10.31	10.82	0.79	–	0.122	0.150
Common Moorhen	18.44	4.77	<0.01	0.23	1.01	2.58	3.32	0.66	0.02	0.01	0.03	10.00	–	1.000
Gull spp.	11.20	6.58	3.35	4.11	5.05	8.12	6.06	4.53	3.68	3.62	5.01	9.58	3.23	–

Binomial tests conducted on interspecific proportions towards other species, as reported in Table 2. Values in the lower left triangle represent the χ^2 test statistic, while the values in the upper right triangle represent the adjusted P values

Table 4 Comparison of models of the time spent in aggressive interactions between swans

Species	Model	k	AIC_c	ΔAIC_c	RL	w_i	ER	R_c^2	R_m^2
Whooper Swans	$i + N + (i|D)$	2	295.87	0.00	1.00	0.505	1.00	0.351	0.193
	$i + (i|D)$	1	296.31	0.45	0.80	0.404	1.25	0.215	0.000
	$i + T + (i|D)$	4	299.29	3.42	0.18	0.091	5.53	0.142	0.129
Bewick's Swans	$i + T * W + (i|D)$	12	802.43	0.00	1.00	0.664	1.00	0.343	0.233
	$i + (i|D)$	1	805.67	3.24	0.20	0.131	5.06	0.226	0.000
	$i + N + (i|D)$	2	807.16	4.74	0.09	0.062	10.68	0.236	0.007
	$i + W + (i|D)$	3	807.74	5.31	0.07	0.047	14.26	0.226	0.000
	$i + T + (i|D)$	4	808.37	5.94	0.05	0.034	19.51	0.211	0.017
	$i + M + (i|D)$	5	808.80	6.37	0.04	0.027	24.16	0.224	0.030
	$i + T + W + (i|D)$	6	810.44	8.01	0.02	0.012	54.83	0.213	0.019
	$i + N + M + (i|D)$	6	810.74	8.31	0.02	0.010	63.75	0.231	0.030
	$i + T + M + (i|D)$	8	811.00	8.57	0.01	0.009	72.75	0.198	0.070
	$i + N * M + (i|D)$	10	813.40	10.97	0.00	0.003	241.39	0.195	0.071
	$i + T * M + (i|D)$	20	820.81	18.38	0.00	0.000	9786.90	0.216	0.091

A summary of the relative support for each of our candidate models of the time spent by swans in aggressive interactions with other swans. Model parameters: intercept (i), number of swans present (N), month (M), winter (W), time of day (T), and observation identity (D). k refers to the number of fixed effects in the model

Table 5 Effect sizes for our best-supported models of Whooper and Bewick's Swan time spent on aggression
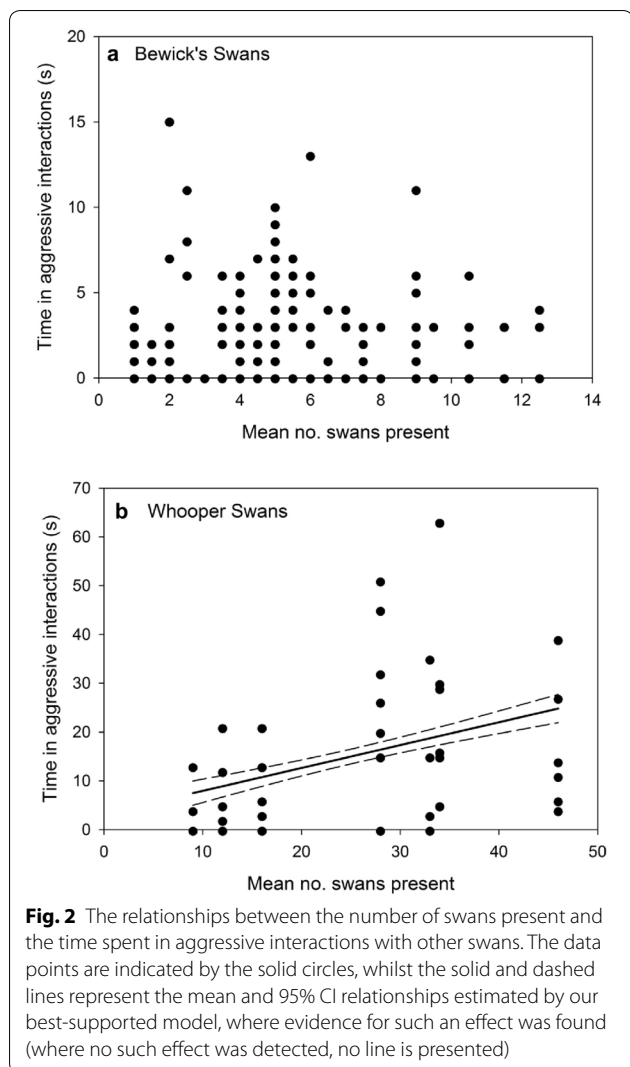
Species	Model	Parameter	Estimate	SE	Variance	SD
Whooper Swans	Conditional	i	1.68	0.70	–	–
		N	0.04	0.02	–	–
		$(i|D)$	–	–	0.17	0.41
	Zero-inflation	i	−1.79	0.82	–	–
Bewick's Swans	Conditional	i	1.09	0.19	–	–
		$T_{(Mid)}$	−0.29	0.29	–	–
		$T_{(P.M.)}$	0.32	0.24	–	–
		$W_{(2019/2020)}$	0.27	0.66	–	–
		$T_{(Mid)}:W_{(2019/2020)}$	0.66	0.82	–	–
		$T_{(P.M.)}:W_{(2019/2020)}$	−2.59	1.03	–	–
		$(i|D)$	–	–	0.15	0.38
	Zero-inflation	i	0.33	0.16	–	–

The mean and SE estimated effect sizes associated with each of the parameters (as defined in Table 4) in our best-supported models of Whooper and Bewick's Swan time spent on aggression. Additionally, the variance (and SD) associated with the random effect of observation identity is also shown

species. For Mute Swans and Whooper Swans, the proportion of aggressive interactions directed towards other birds did not differ from the values observed for smaller waterbirds, although Bewick's Swans showed higher values than 8 of the 13 other species. Taken together, our results were consistent with previous findings that aggression is more likely between individuals with greater overlap in resource use (Peiman and Robinson 2010).

Although the majority of aggressive interactions by swans were directed towards, and received from, conspecifics, we observed some aggression towards 9 of the 11 smaller waterbird species present at the two sites. Only Common Pochard and Common Shelduck were not

observed in aggressive interactions with swans, which may have been due to their low relative abundance at the sites. Given that even the low incidences of aggression observed in our study could carry the risk of serious injury or death, it may seem counter intuitive that smaller waterbirds are so often observed to share habitat with swans. Therefore, smaller waterbirds must balance potential risks of aggression with the possible benefits of sharing habitat or even of associating more closely with swans. Previous studies have found that some smaller waterbird species associate with swans for improved access to food resources, such as submerged aquatic plants that swans bring to the surface (e.g. Bailey and

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Fig. 2 The relationships between the number of swans present and the time spent in aggressive interactions with other swans. The data points are indicated by the solid circles, whilst the solid and dashed lines represent the mean and 95% CI relationships estimated by our best-supported model, where evidence for such an effect was found (where no such effect was detected, no line is presented)

Fig. 3 The mean ($\pm$ 95% CI) duration that swans spent engaged in aggressive interactions with other swans for each **a** winter month and **b** time of day. Data for winters 2018/2019 and 2019/2020 are presented separately

Batt 1974; Beven 1980; Källander 2005). Foraging swans typically bring to the surface more food than they ingest (Gillham 1956), which consequently provides foraging opportunities for other species. Gyimesi et al. (2012) found that commensal foraging with Bewick's Swans doubled the instantaneous food intake rate of Common Pochard. In addition to commensal feeding associations, some smaller waterbird species such as Eurasian Coot may also feed directly on swan faeces (Vogrin 1997; Shimada 2012).

We found mixed support for our *density hypothesis* regarding the influence of swan numbers on the duration of aggressive behaviours. As expected, individual Whooper Swans spent longer in aggressive interactions when more swans were present. However, the relationship between swan numbers and Whooper Swan aggression times was not strong, as the marginal R^2 value
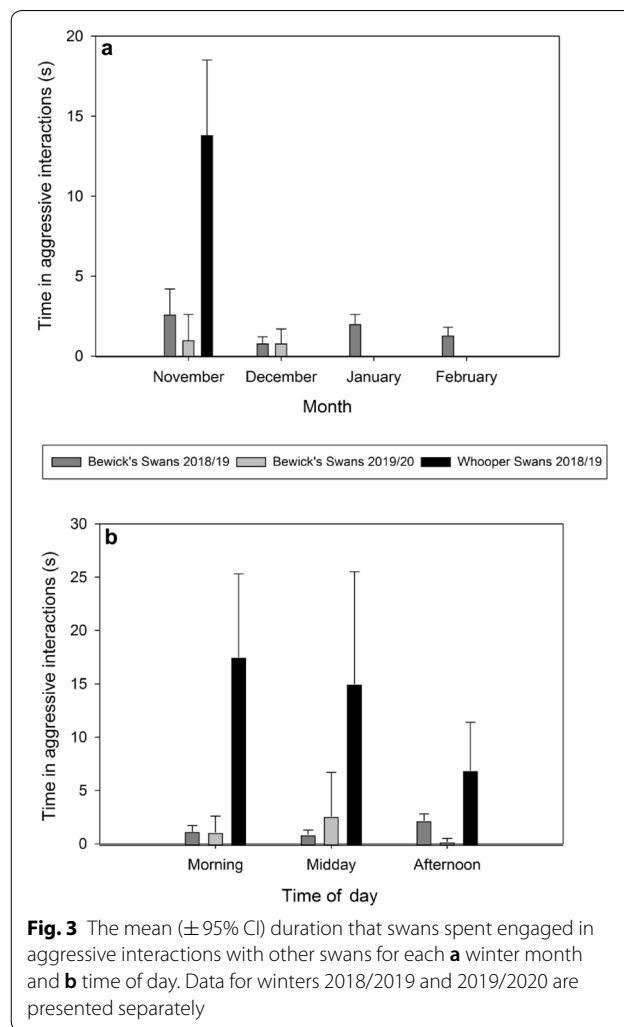
indicated that swan numbers accounted for only 19.3% of the variance in Whooper Swan aggression times. Yet in contrast, Bewick's Swan aggression showed no effect of swan numbers. The reason for these divergent findings may be due to the differences in the ranges of swan numbers recorded at both sites. The mean swan numbers recorded during observations at WWT Caerlaverock, where large numbers of Whooper and Mute Swans overwinter, ranged between 9 and 46 individuals, whilst the mean recorded swan numbers at WWT Slimbridge ranged between 1 and 13 individuals; hence, the number of potential competitors faced by the Whooper Swans at WWT Caerlaverock was markedly higher than that faced by the Bewick's Swans at WWT Slimbridge (Fig. 2). Aggressive behaviours among birds typically become more common as the density of individuals within a habitat increases (Metcalfe and Furness 1987; Wood et al. 2015). It is possible that Bewick's Swans

Table 6 Post-hoc contrasts associated with our best-supported model of Bewick's Swan time spent on aggression

Contrast	Estimate	SE	t ratio	P value
$T_{(A.M.)}{:}W_{(2018/2019)} - T_{(Mid)}{:}W_{(2018/2019)}$	0.29	0.29	1.02	0.912
$T_{(A.M.)}{:}W_{(2018/2019)} - T_{(P.M.)}{:}W_{(2018/2019)}$	−0.32	0.24	−1.35	0.756
$T_{(A.M.)}{:}W_{(2018/2019)} - T_{(A.M.)}{:}W_{(2019/2020)}$	−0.27	0.66	−0.41	0.999
$T_{(A.M.)}{:}W_{(2018/2019)} - T_{(Mid)}{:}W_{(2019/2020)}$	−0.63	0.46	−1.38	0.739
$T_{(A.M.)}{:}W_{(2018/2019)} - T_{(P.M.)}{:}W_{(2019/2020)}$	2.01	0.81	2.49	0.131
$T_{(Mid)}{:}W_{(2018/2019)} - T_{(P.M.)}{:}W_{(2018/2019)}$	−0.61	0.28	−2.21	0.239
$T_{(Mid)}{:}W_{(2018/2019)} - T_{(A.M.)}{:}W_{(2019/2020)}$	−0.56	0.67	−0.84	0.961
$T_{(Mid)}{:}W_{(2018/2019)} - T_{(Mid)}{:}W_{(2019/2020)}$	−0.93	0.48	−1.93	0.388
$T_{(Mid)}{:}W_{(2018/2019)} - T_{(P.M.)}{:}W_{(2019/2020)}$	1.71	0.82	2.10	0.293
$T_{(P.M.)}{:}W_{(2018/2019)} - T_{(A.M.)}{:}W_{(2019/2020)}$	0.05	0.65	0.08	1.000
$T_{(P.M.)}{:}W_{(2018/2019)} - T_{(Mid)}{:}W_{(2019/2020)}$	−0.31	0.45	−0.70	0.982
$T_{(P.M.)}{:}W_{(2018/2019)} - T_{(P.M.)}{:}W_{(2019/2020)}$	*2.33*	*0.80*	*2.91*	*0.045*
$T_{(A.M.)}{:}W_{(2019/2020)} - T_{(Mid)}{:}W_{(2019/2020)}$	−0.37	0.76	−0.48	0.997
$T_{(A.M.)}{:}W_{(2019/2020)} - T_{(P.M.)}{:}W_{(2019/2020)}$	2.27	1.01	2.25	0.217
$T_{(Mid)}{:}W_{(2019/2020)} - T_{(P.M.)}{:}W_{(2019/2020)}$	*2.64*	*0.90*	*2.95*	*0.040*

Parameters are as defined in Table 4. Statistically significant contrasts are in italics

would show increasing durations of aggression with rising swan numbers if observations could be made over a greater range of swan numbers; although with ongoing declines in Bewick's Swan numbers at wintering sites in the UK (Beekman et al. 2019), obtaining such data may prove challenging.

Further comparisons of our models of the time spent in aggressive interactions with other swans found no support for our *winter decline hypothesis*, namely that swans would spend more time engaged in aggressive interactions in early winter months compared with later months. The more limited data collected for Whooper Swans did not allow between-month effects to be tested for, and so only our Bewick's Swan data could be used to test this hypothesis. Our results contrasted with those of Scott (1981), who found that the frequency of aggressive interactions between Bewick's Swans at WWT Slimbridge declined progressively over winter months. The number of Bewick's Swans overwintering at WWT Slimbridge was lower in our study winters than in the late 1970s and early 1980s (Beekman et al. 2019), and so the divergent findings may reflect lower levels of competition in recent winters.

The data that we collected showed that the times spent by swans in aggressive interactions with other swans showed some variation between time of day and between winters for Bewick's Swans. The more limited data collected for Whooper Swans did not allow between-winter effects to be tested for, although no consistent variation

between the three times of day was observed. For our focal Bewick's Swans, for which data could be collected over multiple months in two winters, we found evidence that the time devoted to aggression varied both between times of day and between winters. The tendency for Bewick's Swans to spend less time on aggression with other swans during the afternoon observations in 2019/2020 could be due to the swans spending less time foraging, and hence less aggression linked to competition for food resources. Previous studies of swan behaviour have shown that the most intensive foraging periods for swans typically occur in early morning and before dusk (e.g. Bowler 1996), and thus the afternoon represents a period of low foraging activity. Future research could test for a correlation between foraging activity and aggressive interactions by collecting data on all behaviours as part of a time-activity budget. Our repeated 10-min focal observations showed that Whooper and Bewick's Swans spent means ($\pm 95\%$ CI) of 13.8 ± 4.7 s and 1.4 ± 0.3 s, respectively, engaged in aggression with other swans. These durations were equivalent to 2.3% and 0.2% of the Whooper and Bewick's Swan time-activity budgets, respectively. In this study we focused our explanatory modelling on the interactions between swans, as for all swan species the interactions between swans were more frequent than interactions between swans and smaller waterbirds. However, future research could extend our methodology to examine the time spent by swans on interactions with all waterbird species, as well as the behavioural context of aggression (for example, whether the aggression occurred while both individuals were foraging). Types of food resources represent another potential area for further investigations. At our sites the swans fed on natural vegetation, supplemented by some wheat grains which were provided as part of a public engagement programme (Black and Rees 1984). At other sites swans are known to feed on food items that are buried in aquatic and terrestrial sediment, including pond weed tubers (*Potamogeton* spp.) and root crops such as Sugar Beet (*Beta vulgaris*) (Wood et al. 2019b). The distributions of such cryptic food items are more difficult for the birds to predict, and there may be a higher perceived value of defending profitable feeding patches from competitors. Future research could also therefore assess how the frequency of aggressive behaviours responds to differences in the types of food resources that are available.

Our study provided an example of how questions relating to avian behaviour could be answered using data that were collected remotely via live-streaming webcams. Such remote data collection offers several advantages to researchers, including less disturbance to the focal birds (once the camera has been installed), lower environmental costs (i.e. carbon footprint

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associated with sampling) due to not having to undertake visits to study sites, greater accessibility of research to scientists who cannot physically travel to study sites (either due to logistical difficulties or disability), and the facilitation of citizen science programmes (Eichorst 2018; Schulwitz et al. 2018). Given these advantages, we expect that remote data collection methods will become increasingly popular with researchers. However, our study also highlights a key drawback of such remote data collection, namely the reliability of the technology involved. Malfunctions and environmental damage to the webcams limited the collection of data at both of our study sites, although this did not prevent us from addressing the key questions of our study. Future studies that aim to use remote data collection methods should consider carefully the reliability of both the cameras themselves as well as the stable internet connections required to stream the camera videos. For example, the use of multiple webcams at a single site would provide a buffer against the impacts of the failure of a single camera. We also believe that waterbirds are useful focal species with which to test remote data collection methods, as the birds typically have relatively large body sizes and use open habitat which provides researchers with the unobstructed views required to make reliable identifications of species and accurate assessments of behaviour (Anderson et al. 2011; Peluso et al. 2013).

Conclusions

Our study illustrates how detailed behavioural investigations can help to improve our understanding of the prevalence of aggressive interactions within and between species. Spatially- and temporally-replicated data can allow researchers to identify which species are most commonly involved in aggressive interactions, as well as the frequency and direction of these interactions. Our findings that most aggression was intraspecific and accounted for a low proportion of the total time-budget, together with the lack of strong density-dependence, suggest an absence of any conservation or management issues related to aggression between waterbirds at either site. For example, the behavioural data show that Common Pochard, a species listed as Vulnerable that is undergoing declining population size (Brides et al. 2017), show relatively few aggressive interactions with other waterbirds and none with swans. Conservationists have questioned whether the observed c. 39% decline in winter Bewick's Swan numbers in north-west Europe between 1995 and 2010 may have been at least partially attributable to competition with rising numbers of Whooper and Mute Swans

(Rees et al. 2019). However, our findings show that aggressive interactions from Mute Swans accounted for only 7% of all of the aggressive interactions received, whereas intraspecific aggression from other Bewick's Swans represented 78% of aggression received. Given these findings, it appears unlikely that aggression from Mute Swans has contributed to the observed decline in Bewick's Swan winter numbers. Similar research is now needed at other sites used by Bewick's Swans, including migratory stopover sites and those in the breeding range.

Supplementary information

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