Frequency of kleptoparasitism by Black Brant *Branta bernicla nigricans* on Eurasian Coot *Fulica atra* differs between years and habitats

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Abstract

Although socially parasitic feeding interactions are well documented in birds, kleptoparasitism appears uncommon in geese. Kleptoparasitic behaviour of Black Brant *Branta bernicla nigricans* wintering in northern Japan therefore was studied in 2012/13 and 2013/14. Geese snatched eelgrass *Zostera* sp. from diving Eurasian Coot *Fulica atra* which they had procured underwater. During our observations of 1,615 foraging Brants, when three main foraging tactics (pecking, up-ending and kleptoparasitism) were recorded, kleptoparasitism accounted for 31.5% and 11.7% of the total foraging behaviour in these two winters. The annual variation in kleptoparasitism could perhaps reflect differences between years in the availability and accessibility of food in the same habitats.

Key words: Black Brant, Japan, kleptoparasitism, Sanriku Coast, *Zostera* species.

Birds show a wide range of socially parasitic feeding interactions of which kleptoparasitism is one of the extreme cases (Brockmann & Barnard 1979). During kleptoparasitism, individuals steal food already procured by others to the detriment of the parasitised individuals, in contrast to commensalism where the food lost is not sufficient to have an impact on the host (Iyengar 2008). The phenomenon can occur between individuals both within species and between species (Steele & Hockey 1995; Garrido *et al.* 2002; Galván 2003). It is particularly associated with certain ecological conditions, such as the availability of hosts feeding on large, visible food items and periods of food shortage (Brockmann & Barnard 1979).

In Anseriformes, kleptoparasitism is uncommon (Brockmann & Barnard 1979) compared to some other bird groups, such as gulls and waders (Thompson 1986; Wood *et al.* 2015). Nonetheless, duck species kleptoparasiting coot has been reported in several studies, for instance: Eurasian Wigeon *Anas penelope* taking food from Eurasian Coot *Fulica atra* (Holm & Clausen 2009), Gadwall *A. strepera* from American Coot *Fulica americana* (LeSchack & Hepp 1995) and Mallard *A. platyrhynchos* from Eurasian Coot (Marchowski & Neubauer 2019). These studies show a similar behavioural pattern, in that the ducks kleptoparasitise coots on the water surface, by stealing food that coots bring to the surface from underwater. While we accept that it is impossible to know if coots genuinely suffer from such loss, it is likely that removal of food brought to surface increases the number of dives required for them to achieve the same food intake rate that they would attain in the absence of the kleptoparasite; hence, we use this term rather than considering the behaviour to be commensalism. Kleptoparasitic behaviour enables species to access food that would otherwise not be available to them, albeit that the profitability of such behaviour may vary with social dominance and the general abundance or accessibility of food at the site. LeSchack & Hepp (1995) reported that the rate of kleptoparasitism was greatest for unpaired Gadwall, and Marchowski & Neubauer (2019) showed that the probability of an attack among Mallard was nearly halved when the foraging birds had small rather than large prey items in their bills.

Following an early report from the mid-20th century of food-stealing by Snow Geese *Anser caerulescens* (Jenkins 1944), kleptoparasitism has also occasionally been documented for different goose species. Black Brant *Branta bernicla nigricans* were observed taking food from diving ducks and humans (Einarson 1965; Kirby & Obtrecht 1980), Canada Geese *B. canadensis* take Common Eider *Somateria mollissima* eggs from Herring Gulls *Larus argentatus* (Allard & Gilchrist 2002), and intraspecific kleptoparasitism occurs among Greylag Geese *Anser anser* (Amat 1986). One Light-bellied Brent Goose *B. b. hrota* frequently kleptoparasitised from American Coot in a large flock, ranging from 100–600 birds, at an inland lake in South Carolina (Mcnair 1991). The goose cruised among the flock and frequently stole the part of submerged green algae which the coot brought up to the water surface. Many coot did not show protective behaviour against the goose. However, because Light-bellied Brent Geese were extremely rare in the author's study site, it is not known whether kleptoparasitism by brant species on coot is indeed common behaviour.

In this study, we therefore investigated kleptoparasitic behaviour by Black Brant wintering along the coast of northern Japan on Eurasian Coot (hereafter Coot), describing the frequency of these events in relation to other foraging tactics, and analysing the activity in relation to the birds' environment. The significance of kleptoparasitism for Black Brant is then discussed.

Methods

The study was conducted along 110 km of the southern Sanriku Coast, from Hirota Bay (38.98°N, 141.63°E) through Rikuzentakata City, to the estuary of the Kitakamigawa River (38.57°N, 141.45°E), Ishinomaki City, northern Japan, during the winters 2012/13 and 2013/14 (see Shimada *et al.* 2013). The geese were counted from 72 observation points three times each winter: in December, January and February–March during 2012/13, and in December, January and February during 2013/14. A total of 1,138 and 1,755 brant were counted in 2013/14 and 2014/15, respectively, of which 62.7% and 68.4% were recorded as feeding. The entire survey area was covered by car over 2–3 days on each occasion. Satellite-tracking indicated that no brant were located > 2 km offshore, and tagged individuals were not recorded > 6 km along the coast from their capture site (Shimada *et al.* 2016). The brant generally congregated at specific locations, with few movements of birds between sites, which reduced the likelihood of double-counting. Locations with an unobstructed view of the coast (*e.g.* hill, sandy beach, fishery harbour) were selected for the goose counts, although areas under construction following the 2011 Great East Japan Earthquake were not visited by car because traffic access was suspended whilst the recovery works were underway. Counts were undertaken from sunrise to sunset, and all visible geese were counted using binoculars (> 8×), spotting scopes (> 30×) and hand counters.

During each of the surveys, scan sampling (Altmann 1974) was used to record the foraging behaviour, habitat and microhabitat used by individual birds, with usually one scan sample conducted for each flock encountered, though if focal birds moved out of view before the end of the flock scan the observation was repeated once the birds had settled. Foraging behaviour was grouped into three categories: pecking (surface picking), up-ending and kleptoparasitism. Habitats were divided into three types: fishery harbour, sea (*i.e.* outside the harbour) and sandy beach. Given the time constraints, it was not possible to determine whether the birds were primarily ingesting eelgrass *Zostera* sp. or other food during the surveys. Fishery harbours are usually surrounded by the sea, so some microhabitats occurred within both the sea and harbour habitats. For the fishery harbour habitat, microhabitats were defined as water surface, subsided wharf (caused by the Great East Japan Earthquake; Shimada *et al.* 2013), boat-lift yard and "others" (*e.g.* ropes, cobbled stones and river mouth). In the sea habitat, microhabitats again included water surface and "others" (cobbled stones and river mouth) but also encompassed a sea-farming raft (for a Wakame *Undaria pinnatifida* and Pacific Oyster *Crassostrea gigas* farm) and breakwaters.

Black Brant observed foraging in the sandy beach habitat used just one foraging tactic (see Results), and kleptoparasitism was not observed in these areas, so this habitat was removed from the subsequent analysis.

The number of birds in the study area varies not only between winters but with food availability, with the latter sometimes affected by tide level. Generalized linear mixed models (GLMMs) therefore were used to analyse the effects of the study winter and tide levels on the number of foraging geese that adopted each foraging tactic, for both the sea and fishery harbour habitats. The response variable was the number of foraging geese (recorded as pecking, up-ending and kleptoparasitising) during each survey for each observation point; thus, each observation point has six values for the 2-year study. We allocated a fixed location identity (ID) number to each of the 72 observation points used during the surveys and included this ID factor as the random effect (random intercept) in the model. Fixed effects were the study winter and tide level, with the latter being the tide level recorded at Ohfunato (39.02°N, 141.75°E; Japan Meteorological Agency 2020), near the study area, at the time when we were observing the geese. Large numbers of zeros in the data can cause overdispersion and/or no convergence the model. To avoid the effect of excessive zeros in the analysis, we therefore removed observation points where no Black Brant were recorded in any of the six surveys during the two study winters; *i.e.* the analysis was based on observation points where geese were counted at least once during the two winters. Thus, data from 55 and 40 observation points covering the two main habitats – the sea and fishery harbours, respectively – were included in the analysis. Analyses were conducted separately for each foraging tactic.

The foraging tactic that geese adopted was also affected by microhabitat. To examine the effects of microhabitat on the number of the geese feeding by pecking, up-ending or kleptoparasiting, we set the microhabitat type and tide level as the fixed effects, with the number of foraging geese recorded at each observation point during each survey being the response variable, and with observation point included as a random effect (random intercept). Including the four microhabitat types in each survey, further increased the amount of zero data in our dataset. To avoid the effect of excessive zeros on analysing microhabitat selection by the geese, we therefore again removed data for observation points where no geese were recorded in either of the study winters. Thus data from 41 and 50 observation points were included in analyses of birds foraging within the sea habitat in each study winter, whilst data from 26 and 35 observation points in 2012/13 and 2013/14 respectively were used for analysing goose feeding behaviour in the fishery harbour habitat. Given the different number of observation points providing data for each study winter, we conducted the microhabitat analyses separately for each year.

Despite removing observation points where no geese were recorded there was still an excessive number of zeros in the data. Hence we applied a zero-inflated negative binomial regression model, which analyses count variables with an excess of zeros and has a negative binomial distribution for considering overdispersion in the dataset. Analyses were conducted in Program R version 3.5.1 (R Core Team 2018), using the "glmmADMB" package (Skaug *et al.* 2014).

Results

Kleptoparasitic behaviour

We recorded a total of 1,615 Black Brant foraging in the two main habitats (*i.e.* at sea and in the fishery harbour) during the two study winters (Table 1). The 300 brant seen in the sandy beach area foraged only by pecking in the first winter and up-ending in the second winter, and no kleptoparasitic behaviour was observed in this habitat (Table 1). Hereafter, we report on foraging behaviour in the two main habitats.

Kleptoparasitism accounted for 31.5% of the total foraging behaviour in the first winter (*n* = 692 foraging records in 2012/13); however, in the second winter, its frequency decreased to 11.7% (*n* = 923 foraging records in 2013/14). On the water surface in both the fishery harbour and sea habitats, kleptoparasitic geese always followed Coot and would wait over a recently submerged Coot until it surfaced. They swam directly towards Coot after they surfaced with eelgrass *Zostera* sp. and stole it from them (Fig. 1). Some Coot attempted to retrieve the stolen food, but many of them could not protect their food from the geese, as also documented by Mcnair (1991). Geese usually snatched only part of the food brought to the surface by a Coot, rather than all of the material accessible to them.

Habitat use and the frequency of foraging tactics

Black Brant foraging behaviour (pecking, up-ending and kleptoparasitism) was observed in both of the main habitat categories, on the sea and in the fishery harbour, with 55.8% foraging on the sea and 44.2% in the fishery harbour in the first winter, and 68.1% and 31.9% respectively in the second winter. Pecking was the most dominant foraging behaviour in both habitats each winter, accounting for 42.8% of the total foraging behaviour in 2012/13 and 71.2% in 2013/14. Up-ending accounted for 25.8% of the total foraging behaviour in 2012/13; however, the frequency of this foraging tactic decreased to 17.1% in the second winter. Likewise, kleptoparasitic geese decreased from 31.5% in the first winter to 11.7% in the second winter.

On considering the different types of foraging behaviour for geese in different habitats, incidences of geese pecking in the sea were found to increase from 44.0% in the first winter to 77.1% in the second winter. Incidences of geese up-ending in the fishery harbour habitat during the two winters were 39.5% and 34.0%, and in the sea habitat were 14.8% and 9.2%, respectively. Kleptoparasitic geese in the fishery harbour and sea habitats accounted for 19.3% and 41.2% of the total foraging geese in each habitat respectively during the first winter. However, the following winter, these proportions decreased to 7.5% and 13.7%. Despite the change in the frequency of each foraging tactic, neither study winter nor tide level had a significant effect on \the type of feeding behaviour in the two habitats (GLMMs for the fixed effects of tide and study winter: estimates ± s.e. for geese in the fishery harbour = –0.01 ± 0.01 and –0.30 ± 0.32 on pecking, 0.01 ± 0.01 and –14.85 ± 7.98 on up-ending, 0.01 ± 0.02 and –0.05 ± 0.77 on kleptoparasitism; for geese on the sea = 0.003 ± 0.01 and 1.00 ±

Table 1. Foraging tactics and the number of geese foraging in each habitat and microhabitat during the two study winters.

		Sea				Fishery harbour					
Foraging behaviour	**Winter**	**Water surface**	**Sea-farming raft**	**Breakwater**	**Other**	**Water surface**	**Wharf**	**Boat-lift yard**	**Other**	**Sandy beach**	**Overall total**
Pecking	2012/13	87	90	0	3	2	51	63	10	0	306
	2013/14	273	179	6	27	7	37	108	20	278	935
Up-ending	2012/13	13	23	21	0	14	26	58	23	22	200
	2013/14	4	19	12	23	6	15	74	5	0	158
Kleptoparasitism	2012/13	136	21	0	2	49	10	0	0	0	218
	2013/14	84	2	0	0	22	0	0	0	0	108
Total	**2012/13**	**236**	**134**	**21**	**5**	**65**	**87**	**121**	**33**	**22**	**724**
Total	**2013/14**	**361**	**200**	**18**	**50**	**35**	**52**	**182**	**25**	**278**	**1,201**

Figure 1. Consecutive scenes of kleptoparasitic behaviour by a Black Brant on an Eurasian Coot, illustrating: (a) Coot searching for eelgrass, (b) and (c) Brant approaching the Coot, which is carrying eelgrass, and (d) and (e) Brant snatching part of the eelgrass from the Coot. Photographs by Kenji Satoh.

0.53 on pecking, –0.005 ± 0.003 and 7.6 ± 5.2 on up-ending and 0.02 ± 0.01 and –0.12 ± 0.67 on kleptoparasitism; n.s. in each case).

Some foraging tactics tended to be observed in particular microhabitats, and the effect of microhabitat on the number of geese differed slightly between years (Table 1, Table 2). When on the sea, kleptoparasitic geese tended to be more abundant on the water surface than in other microhabitats (Table 1), and kleptoparasitic activity was significantly lower on the sea-farming raft and "others" habitats than on the water surface (Table 2: $P < 0.01$ for both microhabitats in the first winter; $P < 0.01$ for the "others" habitat in the second

Table 2. Estimates for each coefficient (with mean s.e. values in parentheses), from generalized linear mixed models (GLMM) of the effect of microhabitat on the number of geese that adopted each foraging tactic. Estimates were generated in relation to the "water surface" microhabitat, which was the baseline (reference) category in the model. Analyses were conducted separately for the two main habitats, using data from 41 and 50 observation points for the sea habitat in each of the study winters, and from 26 and 35 observation points for the fishery harbour habitat, in winters 2012/13 and 2013/14, respectively. * $P < 0.05$, ** $P < 0.01$.

	Sea					**Fishery harbour**				
	Microhabitat				**Tide level**	**Microhabitat**				**Tide level**
Foraging behaviours	**Water surface**	**Sea-farming raft**	**Break-water**	**Others**		**Water surface**	**Wharf**	**Boat-lift yard**	**Others**	
Pecking										
Winter 2012/13	0	0.06	–20.63	–3.66**	0.01	0	2.78*	2.72*	0.91	–0.04
		(0.99)	(3106)	(1.34)	(0.02)		(1.26)	(1.15)	(1.35)	(0.01)
Winter 2013/14	0	–1.94**	–4.52**	–2.99**	0.004	0	1.59	2.74**	1.29	0.01
		0.66	0.88	(0.76)	(0.01)		(0.89)	(0.81)	(0.85)	(0.01)
Up-ending										
Winter 2012/13	0	1.21	–1.10	–91.30	–0.01	0	0.51	1.77*	0.08	0.01
		(0.66)	(1.15)	(106000)	(0.01)		(0.97)	(0.85)	(1.08)	(0.01)
Winter 2013/14	0	0.81	3.08	2.33	–0.04	0	0.92	0.89	–1.53	–0.002
		(1.25)	(2.07)	(1.39)	(0.03)		(0.85)	(0.74)	(0.89)	(0.01)
Kleptoparasitism										
Winter 2012/13	0	–1.08**	–15.51	–3.08**	0.02	0	–1.58	–20.70	–20.70	0.0001
		(0.30)	(357.3)	(0.91)	(0.01)		(1.12)	(13800)	(13800)	(0.02)
Winter 2013/14	0	–3.43**	–18.40	–18.40	–0.01	0	–16.34	–16.34	–16.34	0.005
		(1.04)	(1170)	(1170)	(0.02)		(1096)	(1096)	(1096)	(0.04)

winter). Pecking behaviour by geese in fishery harbours was significantly higher in the boat-lift yard microhabitat in both winters (Table 2: $P < 0.05$ in 2012/13, $P < 0.01$ in 2013/14) and in the subsided wharf microhabitats in 2012/13 ($P < 0.05$), while pecking behaviour among geese feeding on the sea habitat was significantly lower among those at the sea-farming raft, breakwater and "other" microhabitats in comparison with geese feeding on the water surface microhabitat, particularly during the second winter (Table 2: $P < 0.01$ for each of the microhabitats in 2013/14). Up-ending by geese in the fishery harbour habitat was more frequently recorded in the boat-lift yard microhabitat during the first winter but not in the second (Table 2: $P < 0.05$ in 2012/13, n.s. in 2013/14). Within the sea habitat, the abundance of up-ending geese was slightly higher at the sea-farming raft and breakwater microhabitats in both winters; however, the differences were not significant. Tide levels also had no significant effect on the number of geese using different foraging behaviours in all analyses (Table 2).

Discussion

Kleptoparasitic behaviour by Black Brant

Although kleptoparasitism has been commonly reported in ducks (*e.g.* Holm & Clausen 2009; LeSchack & Hepp 1995; Marchowski & Neubauer 2019), our observations are the first to suggest this behaviour is a marine foraging tactic commonly employed by Black Brant, at least in our study area. In an unusual freshwater context, Mcnair (1991) suggested that, because Coot must break the surface before eating food, kleptoparasitism was an easy task for Light-bellied Brent Geese *B. b. hrota*. In addition, that author also speculated that the brant used the Coot as "beaters", following them to good foraging areas, and then displacing them. In Mcnair's study, there was only one brant among 100–600 Coot which suggests that this behaviour may have been an exceptional incident.

In our study, kleptoparasitism of eelgrass by Black Brant from Eurasian Coot was commonly observed, with eelgrass being brought to the surface by Coot diving in water that was too deep for the geese to forage in, even by up-ending. Eelgrass is energetically superior to other food resources used by Black Brant (Clausen *et al.* 2002); however, the accessibility of the eelgrass is limited by water levels, with the geese able to reach it at low tide but it becomes almost entirely inaccessible at high tide (Moore & Black 2006; Elkinton *et al.* 2013; Stillman *et al.* 2015). Moreover, eelgrass has a patchy distribution along the coastal study area (Ministry of the Environment 2008), and there are only a few places where the Black Brant have direct access to eelgrass in the region (Takuzo Abe, pers. comm.). Considering the circumstances, kleptoparasitism on Coot (as capable divers accessing food otherwise denied to the geese) represents an effective foraging tactic for Black Brant wintering in our study site. Kleptoparasitism in geese may not be rare if ecological conditions such as availability of hosts feeding on large, visible food items or periods of food shortage (Brockmann & Barnard 1979) are satisfied.

In our study sites, Eurasian Wigeon, as well as Black Brant, frequently kleptoparasitised Coot, but they did not steal from Coot being followed by geese, even though Wigeon were aggressive towards the Coot whereas the geese stole more passively. Randler (2004) reported that Eurasian Coot foraging in close proximity to Swan Geese *Anser cygnoides* could reduce their time spent on vigilance against predators, as well as enhance their food intake rate. In our study area, despite the loss of food to Black Brant, their presence at kleptoparasites could offer a countermeasure against predators, and might also have had the advantage of protecting their own food from more aggressive duck attacks.

Habitat use and the frequency of foraging tactics

The most dominant foraging tactic of the geese in this study, in both habitats (*i.e.* the sea and fishery harbour) was pecking activity. However, in the first winter, kleptoparasitism was more dominant as a foraging tactic than pecking for geese on the water surface microhabitat within the sea habitat. The number of kleptoparasitic geese declined in the second winter, particularly on the sea while the number of pecking geese increased. Although these observations were not statistically significant, we observed that the frequency of foraging tactics among the geese were changed between years. Brockmann & Barnard (1979) suggested that food availability is one of critical factor for plasticity of foraging behaviour.

Black Brant wintering locations are characterised by an abundance of seagrasses and certain marine algae (Reed *et al.* 1998; Lewis *et al.* 2011), upon which they feed, especially on intertidal mudflats in shallow marine waters (Ganter 2000). In the sea habitat within our study area, although sea-farming facilities suffered catastrophic damage following the tsunami in March 2011, farming resumed in the first autumn after the earthquake. As a result, the production of Wakame in 2012 and 2013 recovered to levels 50–60% and 85%, respectively, of those in the year before the earthquake (Fisheries Agency 2014). Food shortage in the first study winter therefore could have induced Black Brant to adopt kleptoparasitism as a strategy, and it could be one reason that tide level showed no effect on the foraging tactics in our analysis. In the second winter, the increase in the extent and number of Wakame farming facilities led to an increase in the area where some periphytic algae could grow. The increasing numbers of geese using pecking feeding behaviour on the sea-farming rafts and water surface microhabitats implies that food availability in the sea habitat recovered following the reconstruction of farming facilities.

In the fishery harbours, most boat-lift yards and wharfs subsided due to the earthquake; these microhabitats therefore were exposed to seawater and were widely covered with seaweed. The gradual slopes of the boat-lift yard allow Black Brant access to food resources obtained by pecking and up-ending regardless of the tidal level. The abundance of seaweed may have increased in the second winter due to decreasing human activity. Thus, the change in food availability between habitats could influence the frequency of pecking and kleptoparasitic behaviour of the geese between years.

The relative energetic costs of different foraging modes could offer a possible alternative explanation for the decreasing kleptoparasitic behaviour in the second winter. In Brent Goose species, the basal metabolic rate (BMR) of swimming is second only to flying, followed by aggression and walking (Clausen *et al.* 2012). Pecking and up-ending behaviours in the boat-lift yard and sea-farming raft habitats involve the energetic costs associated with walking and swimming. However, kleptoparasitic geese have to swim for long time periods and distances to search for, chase, and sometimes attack Coot to snatch eelgrass. Long-term movement and aggressive behaviour would impose higher energetic costs on the Black Brant than pecking and up-ending behaviours. Fewer geese showed kleptoparasitism in the boat-lift yard and the sea-farming raft microhabitats, which contained accessible food but with a lower energy content than eelgrass. Although providing only circumstantial evidence, these observations suggest that Black Brant have to trade-off feeding in habitats where food is easily accessible but of relatively low quality against those with more inaccessible but energy-rich food, or where more energy is expended to attain the same food intake rates.

Reconstruction of damaged fishery facilities has occurred in coastal areas since the Great East Japan Earthquake in 2011, with 85% of farming facilities and 89% of fishery harbours being restored by 2013 and 2019, respectively (Fisheries Agency 2014, 2019). The percentage of Black Brant observed in fishing harbours has gradually decreased as the subsided wharfs following the earthquake were rebuilt (Shimada *et al.* 2018). Original habitats for the geese in our study sites have been reconstructed promptly, but kleptoparasitism by the geese on Coot continues to be observed on the sea (T. Shimada, unpubl. data). This strongly suggests that kleptoparasitism by Black Brant is not an incidental foraging tactic, developed under the unusual environmental conditions following the earthquake, but a normal foraging tactic in this species in response to specific circumstances.

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Photograph: Flock of Black Brant migrating in V formation in Russia, by WWT.