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Trophic relationships between the kelp gull and the Antarctic limpet at King George Island (South Shetland Islands, Antarctica) during the breeding season

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Abstract The diet of the kelp gull (*Larus dominicanus*), its foraging behaviour and the consumption rates on the Antarctic limpet (*Nacella concinna*) were studied during austral spring and summer 1992/1993 and 1993/1994 at Potter Peninsula, King George Island, Antarctica. Prey information was obtained by collecting 237 pellets, foraging behaviour was observed by focal and instantaneous scan samplings, and consumption rate was estimated by means of weekly sampling of limpets found in 5 nests and their respective middens. Limpets were the most important prey followed by scavenged prey (penguin and seal carcasses), amphipods, snails, fish and euphausiids. Foraging gulls spent 51% of the time searching for limpets, 10% moving between foraging areas, 9% in catching effort and 15% handling prey. The number of gulls observed searching for limpets was inversely correlated with the tidal height. In the diet limpets provide 102.3, 159.4 and 188.1 kJ gull^{-1} day^{-1} during incubation, hatching and brooding respectively; these values range between 15 and 27%, with a maximum of 40%, of the basic daily energy requirements of kelp gulls. Total consumption rate estimations for the whole population of gulls at Potter Peninsula reached between 3400 and 4800 limpets day^{-1}, which represents approximately 10–14% of the total annual limpet mortality.

Introduction

The Kelp Gull *Larus dominicanus* is a widely distributed species in South America, Antarctica and sub-Antarctica (Watson 1975). The increases in its distribution and population size are well documented (Fordham 1970; Boekel 1976) and were, in some cases, attributed to the presence of waste of human origin (Crawford et al. 1982). Distributional data suggest that, previous to the current levels of agriculture and industrial production, kelp gulls were much more dependent on intertidal prey than they are now (Fraser 1989). However, the original diet remains unmodified in the Antarctic and sub-Antarctic (Branch 1985; Fraser 1989, among others), as well as in other undisturbed intertidal places (Bahamondes and Castilla 1986).

In Antarctica, kelp gulls are significant predators of the Antarctic limpet *Nacella concinna* in the intertidal zone (Shabica 1976). Previous investigations on the trophic relationships between kelp gulls and limpets in Antarctica and sub-Antarctica were carried out on the Antarctic Peninsula (Shabica 1971, 1976; Maxson and Bernstein 1980; Fraser 1989), South Orkney Islands (Walker 1972; Nolan 1991) and sub-Antarctic Islands (Ealey 1954; De Villers 1976; Simpson 1976; Blankley and Branch 1985; Branch 1985), but no information is available for the South Shetland Islands. However, the variability of characteristics present in the intertidal areas in Antarctica and sub-Antarctica makes some times little comparable the data obtained in other places concerning the effects of environmental factors on prey availability, as in the case of the influence of tides on limpet predation (Branch 1985; Fraser 1989; Nolan 1991). Therefore, the aims of the present work were: (1) to determine quantitatively the contribution of limpets as an energy resource for kelp gulls during the breeding season, and (2) to investigate the role of tidal height in influencing prey availability to gulls at Potter Peninsula.

Materials and methods

The fieldwork was carried out at Potter Peninsula, King George Island, South Shetland Islands, Antarctica (62°14'S, 58°38'W), from 5 October 1992 to 25 January 1993 and from 1 November

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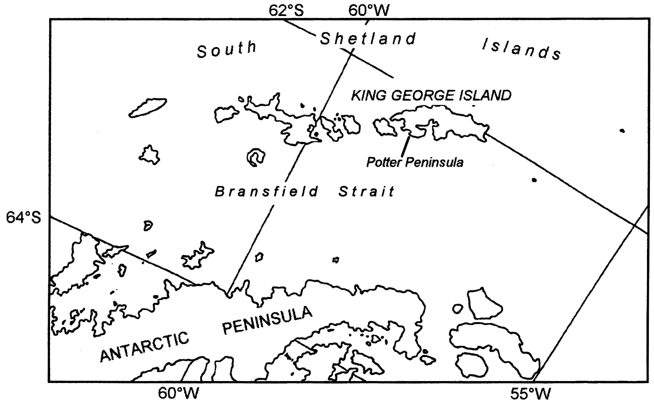

Fig. 1 The location of Potter Peninsula at King George Island, South Shetland Islands, Antarctica

1993 to 30 January 1994 (Fig. 1). Samples were collected throughout the gulls' breeding season. Prey information was obtained by collecting 237 pellets regurgitated by kelp gulls on their breeding territories. Pellets were dissected and prey hard parts identified using a stereo microscope (X20). Additional information on the diet was obtained by systematic observations on foraging behaviour throughout 72 focal animal observations of at least 5-min duration (Altmann 1974), made in the field using a telescope (X12–36). Additionally, 261 instantaneous scan samplings (Altmann 1974) were made at different tidal heights (between 0 and 130 cm) during spring tides, covering 10 foraging places and 65 h of observation.

Estimation of consumption rates of Antarctic limpets was carried out by means of a weekly sampling of shells found in five nests and their respective middens. During each sampling all pellets were collected, totalling 7874 limpet shells between 14 November and 22 December 1993. The weight of the limpets was estimated by using the following calculated regressions(P. Silva):

$$\log WW = 3.666 \log L - 5.089 \; (R = 0.967, \; df = 233)$$

$$\log DW = 3.433 \log L - 5.351 \; (R = 0.914, \; df = 351)$$

for WW = wet weight (g), DW = dry weight (g) and L = shell length (mm).

Results

Diet composition of gulls

The analysis of pellets showed that limpets were the most important prey of the kelp gulls ($F_{[\text{frequency of occurrence}]}$ = 90%), followed by scavenged prey (F = 32%), amphipods (mainly gammarids) (F = 14%), snails (Trochiidae) (F = 11%), nototheniid fish (F = 4%) and euphausiids (F = 3%) (Table 1). Scavenged prey included penguin feathers in 75% of the cases, penguin skin and/or bones in 15%, penguin eggs in 11% and seal skin and/or bones in 32%. There were significant differences in the occurrence of prey items in the diet throughout the breeding season ($\chi^2 = 28.99$, $df = 15$, $P < 0.05$). The importance of amphipods, fish and krill prey decreased from October to January, while limpets and scavenged prey increased in frequency during the same period (Table 1). Algae were present in 17% of the pellets but were considered to be incidental intake, since field observations revealed that gulls frequently catch limpets or snails with little pieces of algae attached to their shells. In addition,two pycnogonids were found partially handled around the sampled nests, and several times gulls were observed foraging on isopods (*Glyptonotus* sp. and *Serolis* sp.) stranded at the beach during low tide.

Table 1 Frequency of occurrence of prey items found in 273 kelp gull's pellets collected from October 1992 to January 1993 at Potter Peninsula

	October	November	December	January	Total
Limpets	81.8	93.4	92.0	84.0	90.3
Amphipods	33.3	15.4	9.1	0.0	13.9
Snails	15.2	8.8	10.2	20.0	11.4
Fish	9.1	2.2	5.7	0.0	4.2
Scavenged prey	15.2	30.8	39.8	28.0	31.7
Euphausiids	6.1	4.4	1.1	0.0	3.0
Sample size	33	91	88	25	237

Foraging behaviour

Gulls observed foraging on limpets in the intertidal area spent 51% of the time searching for limpets, 10% moving between foraging areas, 9% in catching effort and 15% in prey handling. The frequency of catching attempts was 3.36 ± 2.43 attempts min^{-1} [95% CI (confidence interval) = 2.79–3.93, $n = 282$]. Forty-two percent (95% CI = 35–49%) of total attempts observed were successful.

The number of gulls observed searching for limpets was inversely correlated with the tidal height ($r = -0.791$, $P < 0.001$, $df = 20$). In particular, it increased significantly from the lowest height to 1.5 h after this mark during spring tides (Fig. 2). The average number of birds during spring tides in a rocky intertidal shore of ca. 0.03 km^2 where scan samples were performed was 6.3 ± 6.3 ($n = 261$), with a maximum of 65 gulls.

Limpets were captured by three methods. One of them, mentioned hereinafter as "walking" (W) was observed in 13.9% of the cases. This method has never been described for kelp gulls foraging on limpets, and consisted of the search for exposed (not submerged) limpets by walking and their removal by means of several pulls and pecks on the shell up to the dislodgement of the prey from the substrate. However, submerged limpets were also captured by surface seizing (SS) or surface plunging (SP) (Branch 1985; Fraser 1989; see also Harper et al. 1985 for descriptions), which were observed in 60.8% and 25.3% of the attempts, respectively. SS was successful in 40% of the attempted captures, SP in 33% and W in 50% (NS, F = 2.50, $P > 0.05$). Eighty-one percent of the 405 limpets captured were swallowed whole, while the other 19% were brought ashore and meat was pecked from the shells. The length of the limpets swallowed whole ranged from 5 to 46 mm (mean = 26.66 ± 6.43 mm, $n = 7484$), whereas those consumed ashore were sig-

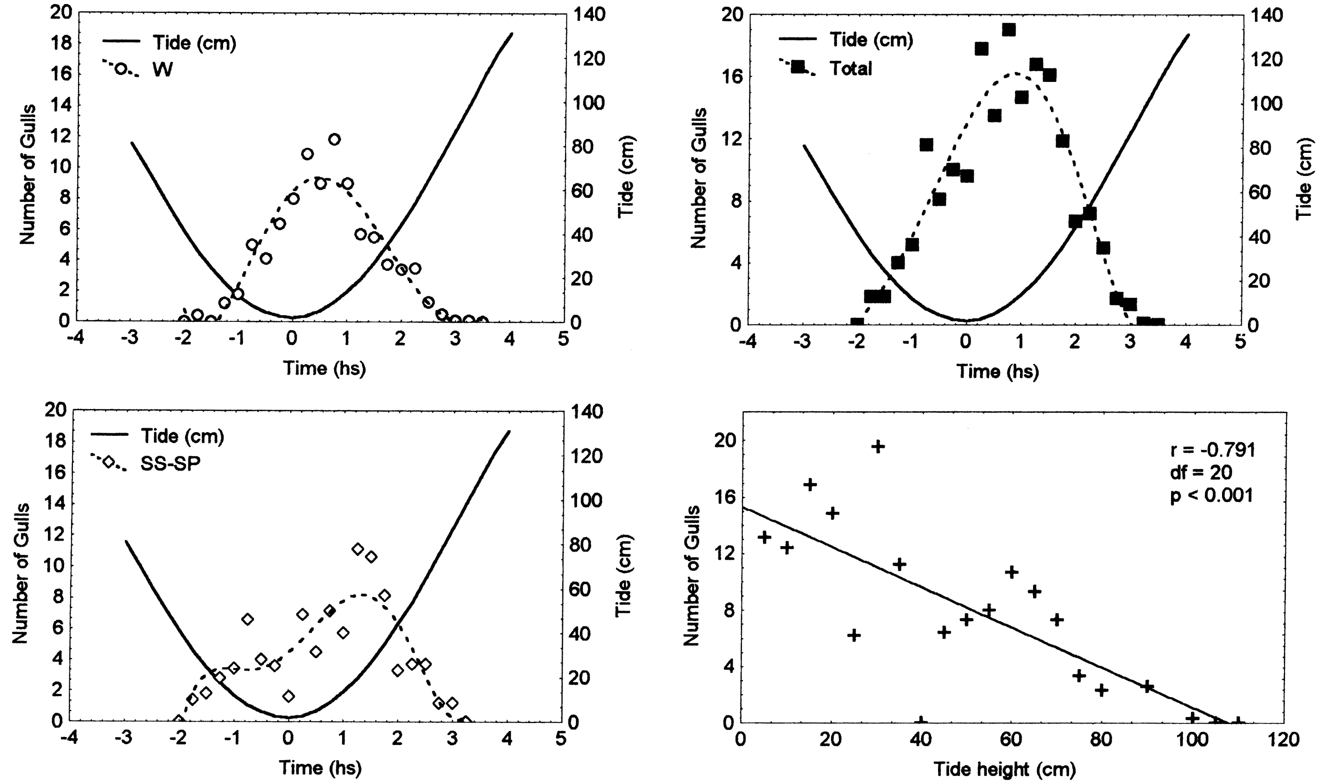

Fig. 2 Number of kelp gulls feeding with different foraging methods on limpets in a rocky intertidal shore monitored in relation to tidal height during spring tides. *Time* = 0 referred to the lowest tide height mark; *SS* surface seize; *SP* surface plunge; *W* walking. Polynomial five-order method used for fitting lines

nificantly larger (T-test = 19.21, $P < 0.001$), ranging from 27 to 54 mm (mean = 35.61 ± 5.22 mm, $n = 388$) (Fig. 3).

Consumption rates

The maximum observed consumption was 35 limpets day^{-1} bird^{-1}, and coincided with the mid-brooding period. No significant differences were found in the mean number of limpets eaten daily per bird during the incubation, hatching and brooding periods: 14 (SE = 3.3, range 4–32), 20 (SE = 4.1, range 8–30) and 17 (SE = 3.9, range 4–35) limpets, respectively (Mann Whitney *U*-Test, $Z > 0.315$, $P > 0.100$, in all cases, $n = 39$). In contrast, the size of limpets captured during the three periods differed significantly (one–way ANOVA, $P < 0.001$): 25.03 ± 5.72 mm during incubation (n = 1468), 25.69 ± 6.01 mm during hatching (n = 3043), and 28.46 ± 6.74 mm during brooding ($n = 3239$). The average weight of the prey differed significantly for the periods considered ($P < 0.001$): 1.38, 1.53 and 2.21 g wet weight (0.28, 0.31 and 0.44 g dry weight) respectively.

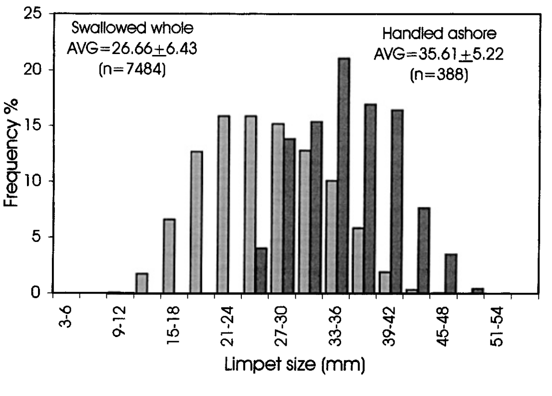

Fig. 3 Length-frequency distribution of *Nacella concinna* shells swallowed whole and handled on shore by kelp gulls at Potter Peninsula

Calculated consumption rates averaged 19.3, 30.6 and 36.7 g (wet weight) bird^{-1} day^{-1} during incubation, hatching and brooding periods, respectively. Using an energetic content of 20.7 kJ g^{-1} (dry weight) given by Blankley and Branch (1985) for *Nacella delesserti* at Marion Island, it is thus possible to estimate daily energetic intakes of 81.8, 127.5 and 150.5 kJ bird^{-1} for the three periods considered, respectively. This estimation was done only with limpets present in feeding piles, but not with those carried ashore, due to the impossibility of assignment to a particular nest. However, focal animal observations revealed that 19% of the limpets were brought ashore individually and consequently were not considered in our computations. Applying this correction with the average size of these limpets to the former estimations, consumption rates reached 102.3, 159.4 and 188.1 kJ bird^{-1} day^{-1} during the three reproductive periods studied, respectively.

Discussion

Diet composition

Limpets were by far the most important prey of the gulls at Potter Peninsula, which is consistent with the importance of patellid gastropods in the diet of this species in other pristine areas where kelp gulls were reported foraging on *Colisella zebrina*, *Scurria scurra* and *Fisurella limbata* in South America (Bahamondes and Castilla 1986), *Nacella delleserti* and *N. macquariensis* in sub-Antarctica (Blankley and Branch 1985; Branch 1985) and *N. concinna* in the South Orkney Islands and the Antarctic Peninsula (Shabica 1976; Fraser 1989; Nolan 1991; Brêthes et al. 1994 among others). Limpets were particularly important prey of kelp gulls in the Antarctic Peninsula during the pair formation, laying and incubation periods (F~84%), while fish (F~8%) and crustaceans (F~4%) occurred less frequently (Fraser 1989). Nevertheless, during the brooding period, limpet importance declined steeply, with a significant increase (F = 92%) in pelagic fish (mainly *Pleuragramma antarcticum*) and krill, which were almost the only prey types offered to the chicks (Fraser 1989). Moreover, Maxson and Bernstein (1984) observed also that in the Antarctic Peninsula low breeding success in gulls occurred when *P. antarcticum* was unavailable to the chicks. These results agree with those reported by Irons et al. (1986) with glaucous-winged gulls in the Arctic, where fish constituted 96% of prey delivered to the chicks. *Pleuragramma antarcticum* was confirmed in the study area because it constituted a common prey for Antarctic terns (M. Favero and P. Silva, unpublished work) and an occasional prey for blue-eyed shags (Coria et al. 1995), but this item was not found in the pellets analysed. Local variations in the abundance of pelagic fish, together with the high abundance of alternative items (e.g. large penguin colonies or krill), may obscure the importance of this prey. The possibility of seasonal variations in the diet was eliminated since data obtained during the following seasons (1994/1995 and 1995/1996) in the same area and Nelson Island (Silva 1996; M. Favero and P. Silva unpublished work) confirmed the importance of intertidal prey compared to pelagic prey during the whole breeding period.

As reported in other penguin colonies at King George Island (Jablonski 1986; Emslie et al. 1995) and agreeing with the occurrence of scavenged penguin prey in the diet of gulls, observations carried out in a pygoscelid rookery located close to the sampling area revealed an intense gull foraging activity among penguin nests.

Foraging behaviour and tidal height

Our results showed that both the number of foraging gulls and their foraging behaviour were strongly influenced by the tides. Since gulls cannot reach prey in the water column at depths greater than one body length (ca. 70 cm, Harper et al. 1985), the number of gulls foraging on limpets was inversely correlated with tidal height; this finding agrees with previous reports (Shabica 1976; Branch 1985; Curtis and Thompson 1985; Irons et al. 1986; Fraser 1989; Nolan 1991). The exploitation curves (Fig. 2) show how the W method closely follows the tidal cycle, while the SS and SP methods seem to be slightly less dependent on this cycle, presenting an extended time of operation of about $1/2 - 1$h before and after the occurrence of the W tactic.

It has been shown experimentally that relaxed or moving limpets are more easily dislodged than those firmly attached (Branch and Marsh 1978; Branch 1985; Davenport 1988). Since the tenacity with which limpets attach to the substrate may influence their availability to gulls, this argument was used to support the hypothesis that gulls forage exclusively by selecting submerged limpets (in movement or relaxed), because these limpets are easier to dislodge than exposed ones as they are strongly attached to the substrate to avoid desiccation (Fraser 1989). The finding that gulls in our study fed successfully on exposed limpets by walking is different from the observation of Fraser (1989), where capture attempts were always directed to limpets below the surface. Our data are in agreement with those of Shabica (1976), who observed gulls occasionally foraging on exposed limpets. The occurrence of the W method can be related to the nature of the observations and the characteristics of the coast; in our study, systematic data were obtained during spring tides which were, on average, 20 cm less high than neap tides. Thus, during the observations, the intertidal area was much more exposed than during the neap tides; scattered observations indicated that the occurrence of walking during neap tides was less frequent than that presented in this work. However, the absence of the W method reported in other areas could be explained by the lack of the extensive rocky intertidal shores with shallow waters that characterize Potter Peninsula.

Consumption estimations

The differences in the estimated daily energy intake between the former two periods (incubating to hatching) and chick care cannot be related to an increase in the daily number of limpets consumed per bird, but to an increase in the mean size of limpets captured. This could be explained by two hypotheses: (1) the fact that large limpets were more available during the third period, or (2) the existence of a positive selection of large limpets by gulls during the chick-rearing period. In relation to hypothesis 1, the increase in the availability of large limpets could be related to differential movements of small and large limpets between the intertidal and the sublittoral, or to a greater visibility of large limpets due to the development of the algal cover during mid- and late summer, which would increase the probability of encounter of larger limpets. Concerning hypothesis 2, field observations revealed that adult gulls frequently feed their chicks by regurgitating the flesh of limpets handled ashore, which, as reported earlier, correspond with larger limpets. Whole limpets (shells included) were offered to the chicks only during the late rearing period. The combined differences in the number and size of limpets consumed throughout the breeding season make a substantial difference in the estimated intakes; during chick rearing our estimations almost doubled the energy intake made during incubation, a variation that could be explained by the needs associated with chick rearing.

Using the equation of existence metabolism (Kendeigh et al. 1977), an adult gull requires a minimum of 703.2 kJ day^{-1}, which means that the limpet resource represents between 15 and 27% of the basic daily energy requirements. The maximum consumption of 35 limpets bird^{-1} day^{-1} (278.9 kJ bird^{-1} day^{-1}) indicates that limpets can supply up to 40% of total daily requirements. Even though not wholly comparable, our data are consistent with the 30% of importance by mass reported by Branch (1985) for *N. delleserti* in the diet of kelp gulls at Marion Island. There is strong historical and biogeographical evidence concerning the relationships between limpets and gulls. Fraser (1989) cites the coincidence, in the southern limits, of the distribution of both species, noting that without limpets, kelp gulls-would probably be unsuccessful in Antarctica and most of the sub-Antarctic islands. Moreover, the presence-absence patterns of distribution of both species in Antarctic and sub-Antarctic areas denote clearly that the presence of limpets in the intertidal represents an-important key attribute for the selection of breeding places (Burger and Gochfeld 1988). However, it has been suggested that during their breeding seasons Arctic and Antarctic larids exploit a greater proportion of oceanic items (as notothenid fish, euphausiids or amphipods in the case of kelp gull) while intertidal prey are mainly captured during the rest of the year (Irons et al. 1986; Fraser 1989). Despite the abundance of oceanic prey during the summer season, their availability is in general more variable than those prey inhabiting intertidal environments. Moreover, Haney and Lee (1994) found that dispersion patterns of gulls during foraging trips offshore are strongly influenced by weather conditions. Therefore it has been suggested that intertidal areas offer more predictable food supplies than oceanic ones do, acting as resource buffers against the great variability of oceanic prey (Ingolfsoon 1976).

Censuses carried out along Potter Peninsula showed the presence of about 200 gulls (including 49 breeding pairs, non breeders and juveniles). Total consumption rate estimations reached between 3400 and 4800 limpets day^{-1}. Considering an intertidal surface of Potter Peninsula of about 0.3 km^2, and a maximum of 9 months of ice-free water, this gives a computed consumption of 3.1–4.3 limpets m^{-2} year^{-1}, which is roughly equivalent to one-quarter to one-third of the estimation made for kelp gulls predating on *N. delesserti* at Marion Island (Branch 1985). Since limpets occur in the intertidal area of Potter Peninsula at a mean density of 32 m^{-2} (Silva 1993), it seems that gulls could account for 10–14% of the total annual limpet mortality. These values are close to the 20% mortality reported by Blankley and Branch (1985) for kelp gulls predating on *N. delesserti* at Marion Island. The predation rate reported not only accounts for important mortality of limpets in shallow waters but could also affect the population structure of limpets throughout the selection of particular prey sizes. Moreover, since limpets were reported to alter algal composition by grazing in a patch, thus maintaining low densities of limpets in exposed areas, gulls can aid algal cover development and indirectly contribute to the maintenance of spatial heterogeneity (Marsh 1986).

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