

INDIVIDUAL DIET DIFFERENCE, PARENTAL CARE AND REPRODUCTIVE SUCCESS IN SLATY-BACKED GULLS¹

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Abstract. In Slaty-backed Gulls, *Larus schistisagus*, some males prey on seabird chicks and deliver these prey to their own broods. Females rarely prey on seabird chicks. Effects of this individual diet variation on reproductive success in relation to parental care behavior were studied on Teuri Island, Hokkaido. Pairs delivering more seabird chicks to their broods raised more fledglings. Their chicks grew faster than those of pairs delivering mostly fish, possibly because energy value of food-loads with seabird chicks was greater than those with fish or marine invertebrates. Timing of breeding, territory size and egg volume also affected reproductive success. The diet variation was not, however, related to these factors. Diet overlap between mates did not affect division of parental care between mates nor reproductive success directly. Males tending to prey on seabird chicks remained more on territory, probably because their food was easily accessible and they foraged more efficiently. This may explain why their mates attended less than other females without decreasing reproductive success.

Key words: *Slaty-backed Gull; individual variation; diet; parental care; reproductive success.*

INTRODUCTION

Individual variation in the diet have been reported in several bird species (Norton-Griffiths 1967, Partridge 1976, Partridge and Green 1985, Herrera 1978, Goss-Custard and Durell 1983, Price 1987). Such variation may affect components of fitness such as the number of offspring produced per breeding attempt, survival rate, and age of first breeding because of short-term advantages in energy intake rate and avoidance of predation (Krebs and McCleery 1984). Although short-term advantages in foraging behavior have been studied in various birds (Stephens and Krebs 1986), few studies have shown that individual diet variations affect survival of parents and offspring (Boag and Grant 1981; Safriel 1985; Pierotti and Annett 1987, 1991).

Larus gulls are appropriate subjects for the study of individual diet variations and reproductive performance because they are generalists at a species level but show individual diet specialization (Harris 1965, McCleery and Sibly 1986, Pierotti and Annett 1987). Among these species, annual and seasonal variations in food

availability affect chick growth and survival, fledgling weight, and vulnerability of chicks to predators through the change in energy and activity budgets (Hunt 1972, Hunt and Hunt 1976, Murphy et al. 1984). Hence, individual diet variations may affect chick survival and growth through differences in (1) energy delivered to chicks and (2) time chicks are unguarded against avian predators. Length of time chicks are unguarded may relate to coordination of nest-relief behavior. Diet differences between male and female parents could affect the sharing of guarding behavior between mates (Niebuhr and McFarland 1983).

Alternatively, individual diet variation could falsely appear to affect reproductive success since it may correlate with other factors affecting reproductive success. The latter include timing of breeding, territory size, egg volume or quality of parents (Vermeer 1963; Patterson 1965; Parsons 1972, 1975; Davis 1975; Hunt and Hunt 1976; Butler and Janes-Butler 1982; Coulson and Porter 1985). Relationships between individual diet variation and these factors require study.

Slaty-backed Gulls (*L. schistisagus*) are dietary generalists. They show large individual diet variation, however, especially among males within the population in Teuri Island in Hokkaido, Japan (Watanuki 1989). This paper reports on (1) the effects of individual diet variation and pa-

¹ Received 23 May 1991. Accepted 9 October 1991.

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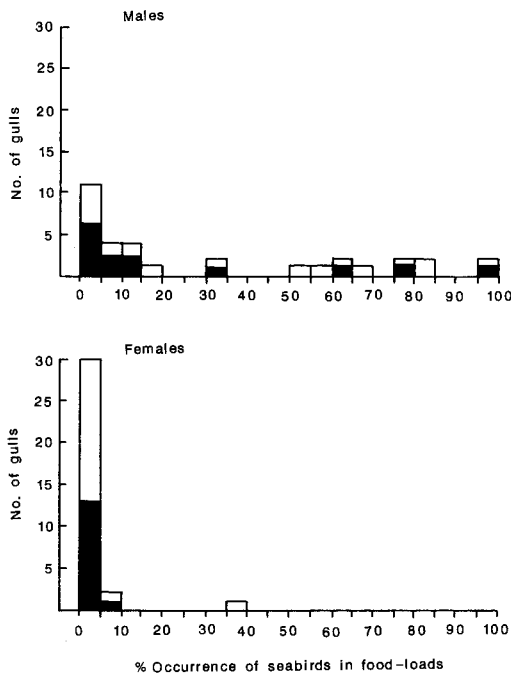


FIGURE 1. Sex and individual differences in predatory habit shown as percentage occurrence of seabird chicks in food-loads delivered to chicks. Black and white bars indicate 1984 and 1985 data respectively. Redrawn from appendix in Watanuki (1989).

rental care behavior on the chick growth and survival and (2) the relationships between male diet and division of parental care between sexes.

STUDY AREA AND METHODS

The study was conducted on Teuri Island (44°25'N, 141°19'E) located 28 km off Haboro, Hokkaido during 1984 and 1985. The island is comprised of steep cliffs reaching 80–100 m above the sea. About 300–400 pairs of Slaty-backed Gulls bred on the cliff ledges, rocky shoulders above cliffs and isolated rock stacks. In addition, about 23,000–29,000 pairs of Black-tailed Gulls (*L. crassirostris*) and 172,000 pairs of Rhinoceros Auklets (*Cerorhinca monocerata*) bred on the island (Watanuki et al. 1988).

A study plot (about 0.15 ha) was established in the center of a subcolony (70–80 breeding pairs) that was situated on a gradual rocky slope sparsely covered with grasses (*Calamagrostis* and *Artemisia*) and strewn with boulders. Nests in the plot were individually marked with numbered wooden stakes when the first egg of each clutch

was laid. I divided the study plot into a 2 × 2 m reference grid with steel poles or paint spots on rocks.

STUDY SPECIES

Slaty-backed Gulls laid eggs (80% of clutches contained 3 eggs) from late April to late May on Teuri Island (Watanuki 1988b). The incubation period was 28 days and first flight of chicks occurred around 45–50 day age (Hashimoto 1977, Watanuki unpubl. data).

These gulls collect pelagic fish (sardine *Sardinops melanosticta* and sand lance *Ammodytes personatus*) at sea and marine invertebrates in the intertidal zone. They scavenge garbage and dead fish (mainly bottom-living species such as rock fish *Sebastes* sp., greenling *Pleurogrammus azonus* and flat fish Pleuronectida). In addition, they prey on nestlings and fledglings of Black-tailed Gulls and Rhinoceros Auklets and nestlings of conspecifics (Watanuki 1989). Large individual diet variation was found within the population. In particular, deliveries of seabird chicks by males to their broods varied among individuals (range from 0%–100%; Fig. 1). Therefore, the correlation of diet and reproductive performance was analyzed.

Although the male predatory habit, as shown by percentage occurrence of seabird chicks in food-loads, did not always show a clear dimorphic pattern (Fig. 1), it may be separated into three groups: 11 males with high scores (>50%), two with medium scores (30–35%) and 20 with low scores (<20%). The analysis of round-trip time and change of parental attendance with respect to breeding stage was treated as dimorphic by excluding the two males with medium scores. The males with high (>50%) and low (<20%) scores are designated as “hunting-biased” and “fishing-biased.” Most females (91%) did not deliver seabird chicks (Fig. 1). However, one female (no. 16 in 1985) frequently preyed on seabirds (36%) (Watanuki 1989). Therefore, this pair was excluded from this analysis.

OBSERVATIONS

During the incubation period, at least one member of 21 (1984) or 23 (1985) pairs in the study plot was marked with picric acid dissolved with ethyl alcohol, using automatic marking devices modified from Burger (1980). Subsequently, sexes of adults were determined from courtship behavior following Tinbergen (1959) and Burger

and Beer (1975). There was no evidence of female-female pairs or trio pairs. Super-normal clutches were not observed.

Study pairs were observed with binoculars (9×35) and a spotting scope (25×60) from a blind placed about 50 m from the edge of the subcolony. The blind was on a slope elevated about 15 m above the study plot, thus allowing wide views. Observations were made every one or two days (usually between 05:00 and 19:00) on calm days between mid-May and late-July. Total time spent in observation during the incubation period was 2,100 and 1,700 nest-hours in 1984 and 1985, respectively. Observation hours during the chick rearing periods totaled 2,400 and 3,900 nest-hours in 1984 and 1985, respectively.

DIET

Each observed food-load delivered to nestlings was assigned to a single category of either fish, marine invertebrates, garbage, or seabird chicks. Species of fish and seabird prey were identified if possible. Fish were further classified into three subcategories of either pelagic, bottom-living or unidentified fish as shown in STUDY SPECIES section. Pairs for which I had at least ten records of food loads by males (14 and 19 pairs in 1984 and 1985, respectively) were included in the analysis. Individual diet variation for females was much smaller than males (Fig. 1). Hence, data of female mates of these males were used even if the female diet sample sizes were smaller than ten. Diet overlap between mates was measured using the overlap index of Pianka (1973)

$$O_{mf} = \sum P_{mi}P_{fi} / \sqrt{\sum P_{mi}^2 \sum P_{fi}^2}$$

P_{mi} and P_{fi} is the proportion of i_{th} diet (fish, marine invertebrates, garbage or seabird chicks) in male and female food loads, respectively.

Food-loads regurgitated by parents were collected and weighed. Two sardines and one Slaty-backed Gull chick of about five days age were collected and frozen. Energy values of sardines and the chick, excluding the inedible feathers, wings and feet, were measured with Shimazu bomb-calorimeter. Energy values of chicks of Black-tailed Gulls and Rhinoceros Auklets were assumed to be the same as that of Slaty-backed Gull chicks. Energy values of other food items were taken from the literature. Since profitability of food for chicks also depends on the handling time, which was defined as the time between food

regurgitation by parents and swallowing by chicks, this parameter was measured in 1985.

PARENTAL CARE BEHAVIOR AND TERRITORY SIZE

I recorded the presence or absence of parents on each territory at 15 min intervals. Incubation and brooding behavior and food delivery to nestlings were also recorded. Parents of Slaty-backed Gulls often reconsume foods regurgitated for nestlings. Food delivery rate was defined as number of territory visits with at least one feeding by a parent.

Parents brooded their nestlings intermittently and at least one parent was on the territory until the oldest chick in a brood attained 10 days of age (see Fig. 4 in RESULTS). The percentage of time spent brooding chicks was calculated until that time ("early chick rearing period") for each parent. The percentage of time both parents were absent from territory was also calculated (following that "late chick rearing period"). Time between departure and arrival of a parent in the territory was defined as "round trip time." Percentage of time both parents were on territory and the time chicks were unguarded were calculated as measures of the coordination of parental care between mates (Reid 1988). If we assume that one parent at the nest is necessary and sufficient to protect the young, then the presence of two parents at the nest is inefficient because neither parent is foraging at the time (Nur 1984).

Locations of territorial behaviors such as aggressive upright, stem pulling and attacks (Tinbergen 1959) were recorded on the map of study plot referring the 2 × 2 m grid during the pre-laying and the early nestling periods. A territory was defined as the minimum convex polygonal area formed by connecting the outermost boundary localities of these behaviors.

REPRODUCTION

The study plot was visited every five days from mid-April to early August to record laying and hatching dates, egg size, presence of chicks, and mass of chicks. Eggs were individually marked with ink. Hatchlings were individually marked with numbered, colored leg bands. Length (L) and width (W) of eggs were measured to nearest 0.1 mm with vernier calipers. Egg volume (V) was estimated by the formula:

$$V = 0.476 \times L \times W^2 \text{ (Harris 1964).}$$

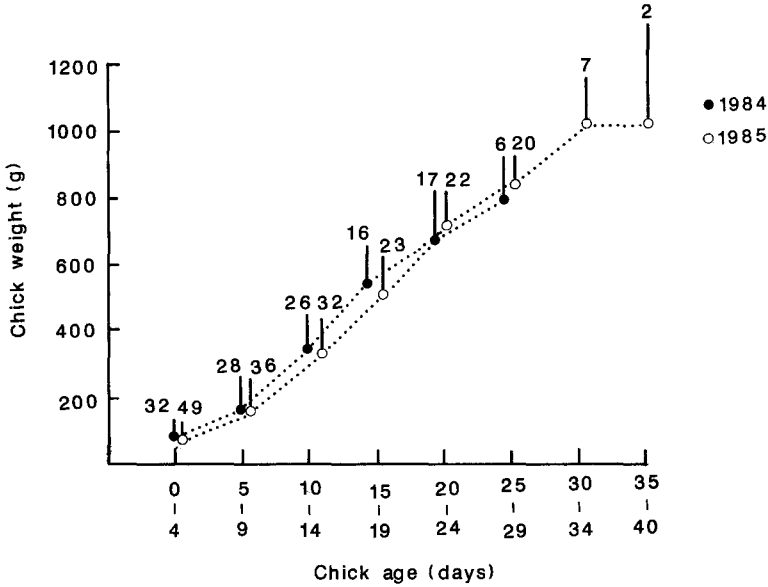


FIGURE 2. Chick growth shown by mean and 1 SD with sample size.

Mean egg volume within a clutch was used as a representative of the clutch.

Large chicks moved and hid away from their nests during visits. Hence, their survival was monitored during behavioral observations. Chicks were weighed with a spring balance to the nearest 5 g. Chick growth rate (g day^{-1}) was defined as the slope of the linear regression line between 5 and 20 days of age. This is a period during which the chicks of large gull species grow almost linearly (Fig. 2, see also Vermeer 1963, Spaans 1971, Hunt and Hunt 1976). Mean chick growth rate within a brood was used as representative of the brood. If only one chick's growth within a brood was measured (7 cases among 29 broods), I used it as representative of that brood. Fledgling mass could not be measured as I did not capture chicks near fledging age. The chicks were assumed to fledge at 45 days of age.

There were no significant differences between years in egg laying date, clutch size, brood size, chick survival, and chick growth rate (Watanuki 1988b; see Fig. 2 also). The proportion of hunting-biased males did not differ between 1984 and 1985 (Fig. 1, $\chi^2 = 1.19$, $df = 1$, ns), therefore the data for both years were combined. Nonparametric statistical tests were used (Mann-Whitney *U*-test and chi-square test). An exception was that an approximate test of significance of the Spearman's rank correlation (r_s) was determined using a *t*-test (Sokal and Rohlf 1981).

RESULTS

REPRODUCTIVE SUCCESS

Chick growth and survival were better in pairs delivering more seabird chicks to their broods (Table 1, Fig. 3). Pairs delivering seabird chicks more than 10% in their food-loads produced twice as many fledglings as those delivering seabird chicks less than that. Chick growth rate of the former was about 1.5 times that of the later (Fig. 3). The proportion of seabird chicks in food-loads brought by each pair was largely determined by the food brought by the male parents of that pair ($r_s = 0.97$, $df = 31$, $P < 0.01$).

Pairs having larger territory or hatching eggs earlier produced more fledglings (Table 1, Fig. 3). The amount of time chicks were unguarded correlated positively with both number of fledglings and chick survival. Neither food delivery rate nor brooding time affected production of fledglings, chick survival, or chick growth (Table 1). Growth rates of chicks hatched from clutches with larger egg volume were higher. Diet overlap between mates correlated negatively both with number of fledgling and with chick growth (Table 1).

CORRELATION AMONG BREEDING BIOLOGY TRAITS

Independence of individual diet variation from other aspects of breeding biology was tested by

TABLE 1. Relationships between occurrence of seabird chicks in the diet brought by pairs, territory size, hatching date, time chicks were unguarded, food delivery rate by pairs, time chicks were brooded, the mean egg volume, and diet overlap between mates, and the number of fledglings, chick survival until fledging and chick growth rate as shown by Spearman's rank correlation coefficient (r_s) with sample size in parentheses. Approximate test of significance of the coefficient was done by t -test and indicated by ** ($P < 0.01$) or * ($P < 0.05$). The maximum sample size is 33 but it differs in some cases since some parameters could not be measured for a few pairs.

	Reproductive success		
	No. fledglings	Chick survival	Chick growth
Seabird chicks in diet	0.38 (33)*	0.36 (33)*	0.39 (29)*
Territory size	0.51 (27)**	0.46 (27)**	0.35 (24)
Hatching date	-0.43 (33)*	-0.41 (33)*	-0.25 (29)
Time chicks unguarded	0.63 (32)**	0.60 (32)**	0.35 (28)
Food delivery rate	0.32 (33)	0.19 (33)	-0.33 (29)
Time chicks brooded	0.05 (30)	0.07 (30)	-0.04 (26)
Egg volume	0.08 (31)	0.05 (31)	0.45 (27)*
Diet overlap	-0.34 (33)*	-0.37 (33)*	-0.45 (29)*

correlation analysis. There were no significant correlations between the proportion of seabird chicks in the food-loads brought by pairs and hatching date, territory size, food delivery rate, time chicks were unguarded, time chicks were brooded or egg volume (r_s ranged from -0.27 to 0.34 and none were significant). However, egg volume correlated positively with territory size ($r_s = 0.54$, $df = 23$, $P < 0.05$).

Diet overlap between mates was not related with any measure of coordination of chick guarding (r_s ranged from -0.30 to 0.12, none were significant). Diet overlap between mates correlated negatively with the proportion of seabird chicks in food-loads brought by males ($r_s = -0.85$, $df = 31$, $P < 0.01$). This indicates that individual diet variation in males was a major factor determining diet overlap between mates.

MALE AND FEMALE PARENTAL CARE

There were negative correlations between males and females in incubation time ($r_s = -0.98$, $df = 29$, $P < 0.01$) and in the time on territory both during the early ($r_s = -0.56$, $df = 29$, $P < 0.01$) and late chick rearing periods ($r_s = -0.47$, $df = 30$, $P < 0.01$). Eggs were covered at all times. However, there were no significant correlations between mates in either time on territory during the incubation periods ($r_s = -0.32$, $df = 29$, ns) or in the food delivery rate ($r_s = 0.26$, $df = 31$, ns). Brooding time of males positively correlated with that of females ($r_s = 0.50$, $df = 28$, $P < 0.01$).

Changes in parental care with respect to breeding stage are shown in Figure 4. Hunting-biased

males spent more time on territory in the late chick-rearing periods than either their mates or fishing-biased males. There was no significant difference in time on territory between fishing-biased males and their mates in most of the breeding stages. Females of hunting-biased pairs spent less time on territory than females of fishing-biased pairs in the last half of the late chick-rearing periods.

Time spent brooding the nestlings decreased during the first 10 days from hatching (Fig. 4). Length of time chicks were unguarded increased during the late chick-rearing periods, especially after the oldest chick attained 20 days of age. There were no significant differences between either males and females or between hunting-biased and fishing-biased pairs in the percentage of time spent incubating, brooding and time chicks were unguarded, with one exception (Fig. 4). Males fed their nestlings about 1.5 times more frequently than females in both hunting-biased and fishing-biased pairs (Fig. 4).

ROUND TRIP

Round trips of hunting-biased males were shorter than those of their mates in all cases except for trips when parents delivered marine invertebrates (Fig. 5). In fishing-biased pairs, however, round trips of males did not differ from those of females.

The round trips of hunting-biased males were shorter than that of fishing-biased males for most of the cases. Although the trips of females of either hunting or fishing-biased pairs did not differ in most cases, trips without food or those with

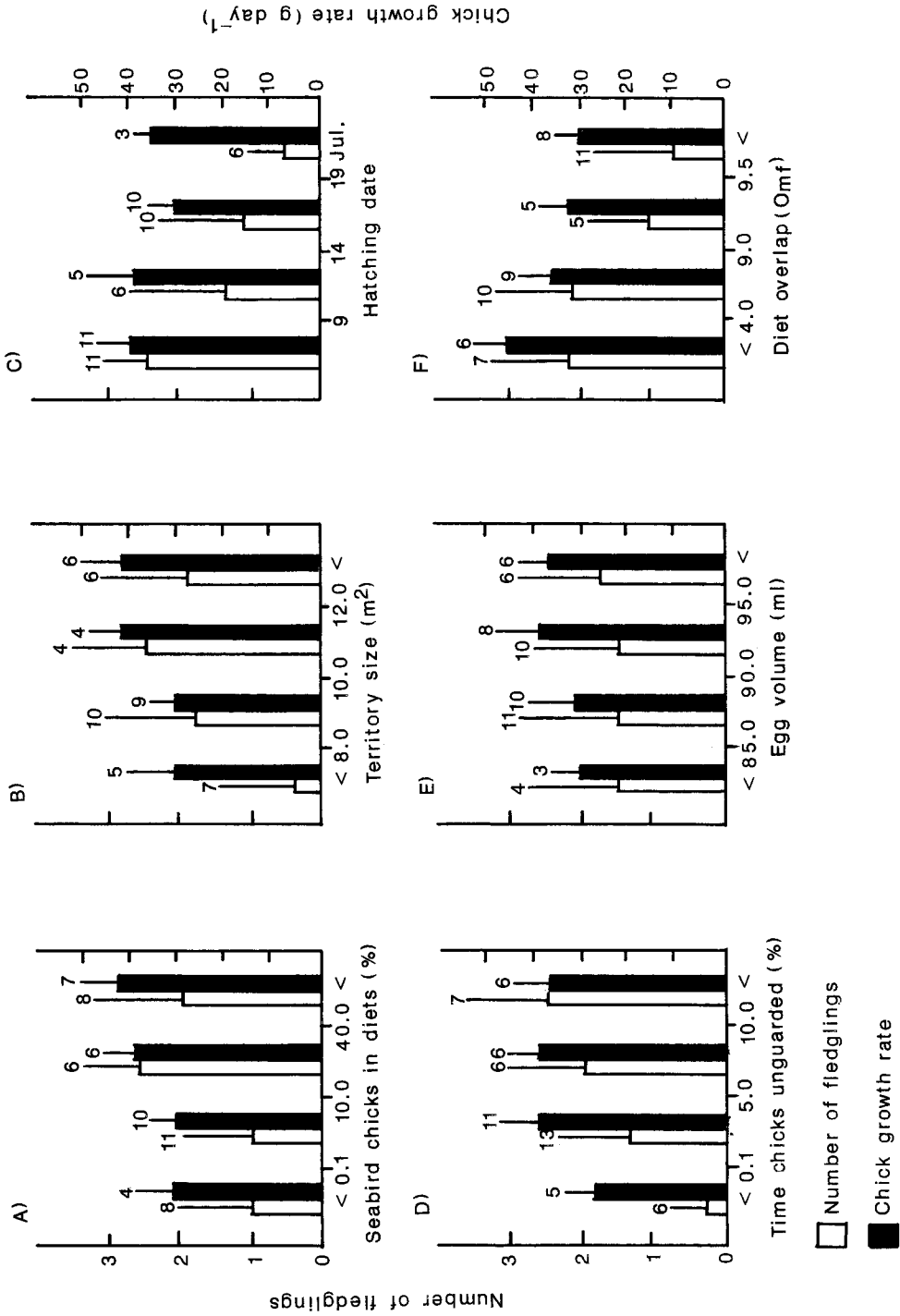


FIGURE 3. Effects of (A) the occurrence of seabird chicks in diet brought by pairs, (B) territory size, (C) hatching date, (D) time chicks were unguarded, (E) the mean egg volume within a clutch, and (F) diet overlap between mates on the number of fledglings per pairs and chick growth rate. Sample sizes are at the top of 1 SD bars.

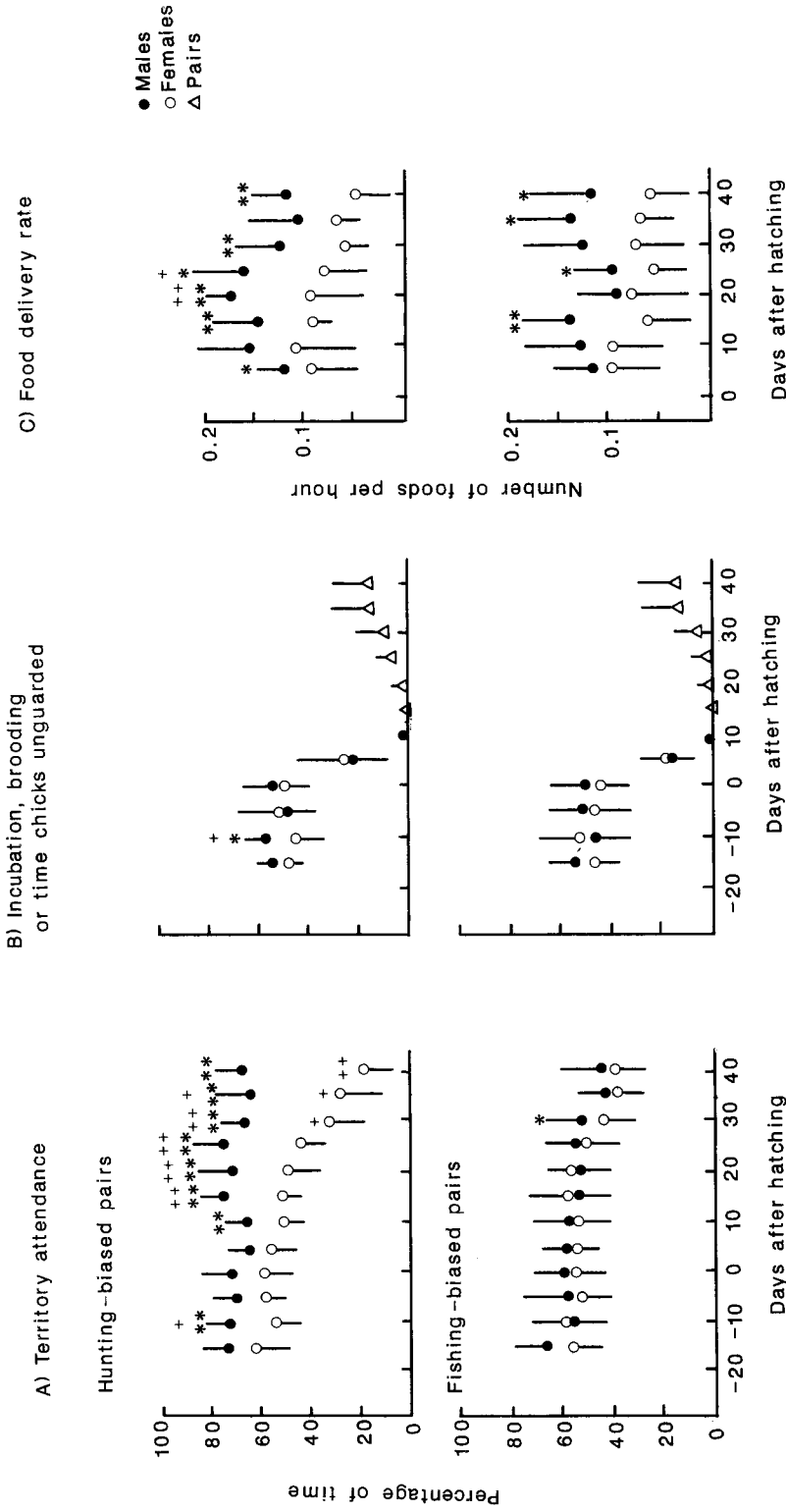


FIGURE 4. Differences in parental care behaviors between males and females (significant differences are indicated by *) or between hunting-biased and fishing-biased groups (significant differences are indicated by +). The mean and 1 SD are indicated. Number of pairs observed was 3-9 for hunting-biased pairs and 6-18 for fishing-biased pairs. Significance was determined by Mann-Whitney *U*-test and indicated by */+ or **/+ +, $P < 0.05$ or **/+ + +, $P < 0.01$. Triangles indicate time chicks were unguarded.

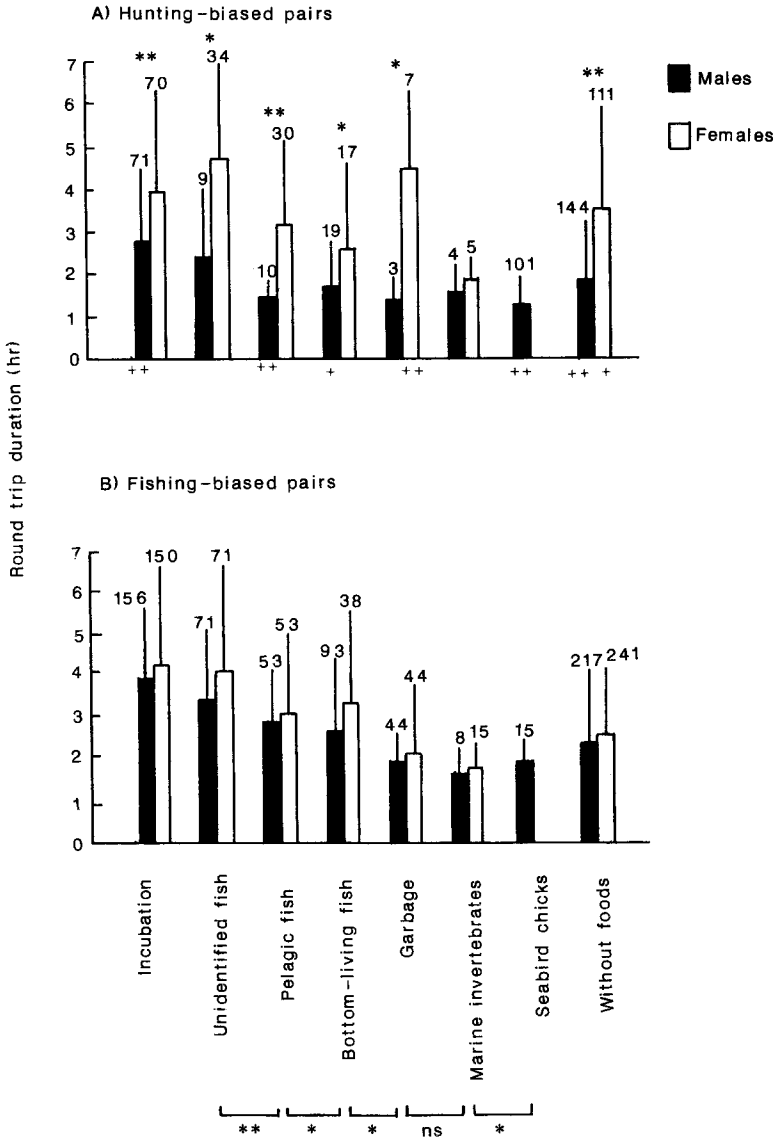


FIGURE 5. Duration of round trips during the incubation and chick rearing periods in relation to food items delivered to chicks. The mean and 1 SD are indicated with sample sizes on top of the bars. Significant differences between males and females or those between hunting-biased and fishing-biased groups were examined by Mann-Whitney *U*-test and indicated by * and +, respectively (* or +, $P < 0.05$; ** or ++, $P < 0.01$). Significances between food types are indicated by * ($P < 0.05$) or ** ($P < 0.01$).

garbage for females of hunting-biased pairs were longer than those of females of fishing-biased pairs.

When data were combined for both parents, the round trips when parents delivered foods for their broods were in the following order: unidentified fish > pelagic fish > bottom-living fish

> garbage = marine invertebrates > seabird chicks (Fig. 5).

Parents did not always deliver foods following round trips. Proportions of the trips yielding foods did not differ between hunting-biased (50%) and fishing-biased males (57%) ($\chi^2 = 2.95$, $df = 1$, ns) or between females of hunting-biased (46%)

TABLE 2. Wet weight of food-loads (mean \pm SD g and sample size in parentheses), energy density (kJ g⁻¹ wet weight) and calculated energy value of a food-load with each type of prey (kJ).

Food type	Wet weight	Energy density	Energy value
Sardines	37.8 \pm 20.0 (6)	10.5 ^a	396.9
Sandlances	16.7 \pm 10.8 (4)	6.7 ^b	111.9
Rock fish	52.8 \pm 5.9 (5)	5.0 ^{b,c}	264.0
Marine invertebrates	21.7 \pm 8.9 (3)	2.6–3.4 ^{c,d}	56.4–73.8
Black-tailed Gull chick	88.8 \pm 33.8 (4)	6.6 ^{a,f}	586.1
Rhinoceros Auklet chick	127.2 \pm 42.9 (9)	6.6 ^{a,f}	839.5
Entrails of seabirds	50.0 (1)	10.9 ^e	545.0
Garbage	45.2 (1)	12.6 ^e	569.5

^a This study.

^b Harris & Hislop (1978).

^c Hunt (1972).

^d Sibly and McCleery (1983).

^e Kagawa (1986).

^f Energy value of Black-tailed Gull and Rhinoceros Auklet chicks was assumed to be the same as Slaty-backed Gull chicks. Feet and wings of seabird chicks were unedible parts and removed for calculation of energy value.

and fishing-biased pairs (48%) ($\chi^2 = 0.29$, $df = 1$, ns). When the data for fishing-biased and hunting-biased are combined, males yielded food-loads more frequently than females ($\chi^2 = 7.54$, $df = 1$, $P < 0.01$).

DIET QUALITY

The mean mass of food-loads composed of seabird chicks was greater than that containing even the largest fish (rock fish) (Table 2; $U = 57$, $P < 0.01$). Calculated energy value of food-loads (energy density \times mean weight of food load) was in the following order: seabird chicks > garbage and entrails of seabirds > fish > marine invertebrates (Table 2). Energy content of garbage, which was estimated by only one food-load, probably varied depending upon the type of refuse. However, garbage was not very important (2–20%, calculated from Fig. 5) in the diet delivered to chicks.

Slaty-backed Gull chicks had difficulty swallowing seabird prey because these food-loads were large and gull chicks could not tear these prey. Handling time (mean \pm SD) of food-loads with seabird chicks (156 \pm 106 sec, $n = 16$) was longer than that of fish loads (26 \pm 37 sec, $n = 72$; $U = 121$, $P < 0.001$).

Repeat feedings was recorded for hunting-biased pairs in 1985. Repeat feedings occurred more frequently when males delivered seabird chicks for their own broods (66/69) than when they and their mates delivered fish (20/64; $\chi^2 = 60.36$, $P < 0.001$ for males and 21/107; $\chi^2 = 97.05$, $P < 0.001$ for females). During these feedings, intruders of Slaty-backed Gulls pirated food seven times.

DISCUSSION

DIET AND SUCCESS

Individual diet variation may affect chick growth and survival through energy delivery or chick guarding time. Although territory size, hatching date and egg volume affected chick survival or growth, the diet variation was not related to these factors.

In Herring Gulls (*L. argentatus*), seabirds or garbage specialists obtained energy at a higher rate than mussel or starfish specialists (Sibly and McCleery 1983, Pierotti and Annett 1991). Pierotti and Annett (1991) suggests that energy may not be the proper currency for examining diet choice in Herring Gulls subject to a variety of constraints. In Slaty-backed Gulls, however, diet choice was directly related to chick survival and growth.

Pairs delivering more seabird chicks raised faster growing chicks and produced more fledglings (Table 1). Food delivery rate was not related to the individual diet variation. Assuming that mass of food-load for each type of prey is independent of diet variation, pairs delivering more seabird chicks containing more energy than fish or marine invertebrates could therefore offer more energy to their chicks.

Time guarding eggs and chicks against avian predators such as crows and conspecific adults (Parsons 1971, Davis and Dunn 1976, Montvecchi 1977) affects reproductive success (Hunt 1972, Hunt and Hunt 1976, Pugsek 1983, Sibly and McCleery 1985). Guarding time could be related to coordination of nest relief behavior

between mates (Coulson 1966, Niebuhr and McFarland 1983).

In Slaty-backed Gulls, the individual diet variation was not related with time chicks were unguarded. The positive correlation between the time chicks were unguarded and the number of fledglings, which is found also in Great Black-backed Gulls, *L. marinus* (Butler and Janes-Butler 1982), is possibly artificial. The time the chicks were unguarded increased in the later chick-rearing period (Fig. 3), as occurs in other species of gulls (Butler and Trivelpiece 1981, Pugsek 1983). Therefore, the longer the chicks survived, the more they were left unattended.

Diet overlap between mates was inversely related to reproductive success. Different types of food of Herring Gulls are available at different times of days (Sibly and McCleery 1983). Hence, as male and female members of pairs differ in their feeding specialization, they relieve incubation duties in a coordinated fashion (Niebuhr 1983, Niebuhr and McFarland 1983). Assuming that one parent at the nest is necessary and sufficient to protect the young, then the presence of two parents at the nest is inefficient. The time both parents are on nests and the time chicks are unguarded are therefore indices of coordination of parental duties between mates (Nur 1984, Reid 1988). In Slaty-backed gulls, these two indices of coordination were independent with diet overlap, indicating that diet overlap does not affect coordination of parental duties. Diet overlap increased with the occurrence of seabird chicks in diet. Therefore, the relationship of diet overlap with reproductive success may be misleading.

Finally, the "quality" of males may contribute to individual variation both in the diet and reproductive success. Individual diet variation in males determined most of the variation of the diet brought by pairs. There is considerable variation in "quality" of individuals in Black-legged Kittiwakes, *Rissa trydactyla*, which is the most important factor determining reproductive success (Thomas and Coulson 1988). "Quality" of individuals may be genetically correlated with the ability of their offspring (Coulson and Porter 1985).

Hunting-biased males spent less time foraging than fishing-biased males, but delivered foods to their nestlings as frequently as the latter. Hunting-biased males may be more efficient in obtaining food than fishing-biased males. Seabird chicks are available around the subcolony, while

fish are available at sea or at docks away from the subcolony. Therefore, the gulls may possibly fly longer distances in search for fish than they do for seabird chicks. Hence, hunting-biased males forage easily accessible prey. Moreover, the foraging trips of hunting-biased males were shorter than fishing-biased males for most of the food items as well as during the incubation periods (Fig. 4). This indicates that hunting-biased males may be more effective foragers than fishing-biased males. The proportion of gull chicks in the food-loads containing seabird chicks was higher among hunting-biased males than fishing-biased males (Watanuki 1989). Gulls protect their offspring and gull chicks defend themselves against Slaty-backed Gulls, hence gull chicks are probably difficult prey to kill (Watanuki 1989). This indirect evidence suggests that hunting-biased males forage more efficiently and are more skillful at killing seabird chicks than fishing-biased males.

The reason why hunting-biased males stayed in the territory longer instead of delivering foods more frequently than fishing-biased males is unclear. Slaty-backed Gull chicks could not easily swallow seabird chicks. Therefore, parents delivering seabird chicks to their own nestlings often reconsume prey, probably to avoid piracy.

Among gull species, individual differences in diet choice, foraging efficiency, reproductive success and parental care behavior may depend on age (Pugsek 1983, Greig et al. 1983, Reid 1988). Pierotti and Annett (1991) suggest that old Herring Gulls are mussel specialists. Relationships between age and such traits remain to be studied in Slaty-backed Gulls.

SHARE OF CARE BETWEEN MATES

In monogamous seabirds, the sharing of parental care between sexes depends on the ability of parents to provide additional parental care, investment in other aspects of reproduction such as gamete production, nest construction and territory defense, the probability of remating after desertion of their mates and offspring and the value of additional care to young (Montevecchi and Porter 1980, Pierotti 1981, Burger 1981, Butler and Janes-Butler 1983, Wiggs and Morris 1987). In addition to these factors, individuals differences in foraging behavior could affect the sharing of parental care between mates in Slaty-backed Gulls.

Houston and Davies (1985) suggest that in birds with biparental care, individuals will work less if their mates do more for raising offspring. Hunting-biased males attended territories more than others and their mates attended less than females paired with fishing-biased males in the late chick-rearing period. However, food delivery rates did not differ between females paired with hunting-biased and fishing-biased males. Hence, females paired with hunting-biased males could spend more time outside of the territory and rest or forage more than females paired with fishing-biased males. Thus, females paired with hunting-biased males might invest less effort in reproduction and be able to raise more fledglings than females paired with fishing-biased males.

SIGNIFICANCE OF PREDATORY HABIT

About one-third of males and most females did not prey on seabird chicks. Seabird chicks contain high energy and pairs delivering more seabird chicks produced more fledglings. Why did all the gulls not specialize as seabird hunters? The following are three possible hypotheses: (1) predation on seabirds is currently spreading in the Teuri population, (2) life-time reproductive success of gulls preying upon seabird chicks does not differ from those foraging on fish because, although the latter produce fewer fledglings, their survival may be higher, (3) immigration from other colonies dilutes the spread of the predatory habit.

The occurrence of seabird chicks in pellets and food remains collected at the study plot did not increase between 1979 and 1985 (Watanuki 1988a), suggesting that the predatory habit has not been spreading recently. Long-term changes have yet to be studied for examining this hypothesis more clearly.

Transmission of food habits from parents to offspring is suggested for several species of birds (Partridge and Green 1985 for review). Postfledging survival and adult survival are two components of life-time reproductive success. Coulson and Porter (1985) found that chick growth rate is positively correlated with post-fledging survival in Black-legged Kittiwakes. In Slaty-backed Gulls, predatory habit correlated positively with chick growth rate and therefore maybe correlated with post-fledging survival. Hunting-biased males spend much time in territories and might be more vulnerable to land-based predators. However,

there are no effective land-based predators of adult seabirds on the island. Although Black-tailed Gulls swoop and assault Slaty-backed Gulls attacking their offspring (Watanuki 1983), they did not injure the Slaty-backed Gulls. No parents disappeared during the study seasons.

In the Yururi and Daikoku colonies in east Hokkaido, 80–83% of the food delivered to chicks were fish and only 0–5% were seabird chicks (Watanuki 1988a). Immigration of gulls, which are unlikely to specialize in preying upon seabirds, from other colonies into Teuri population might dilute the spread of predatory habit. Although the chick survival and growth are not greatest on Teuri Island in comparison with Daikoku and Yururi Islands (Watanuki 1988b), the annual population increase in Teuri (19.3%) is greater than Daikoku (12.6%) or Yururi (5.0%) (Watanuki et al. 1988). This indicates that immigrants establish territories in Teuri or that adults and fledglings in Teuri population survive better than others.

In conclusion, individual diet difference partly affected reproductive success. This may be because of the high energy value of food loads with seabird chicks. Males tending to prey on seabird chicks guarded their own chicks longer but delivered foods as effectively as others. They may also have high foraging efficiencies and increased abilities to kill seabird chicks. This may explain why their mates spend less time in the territory than others without decreasing reproductive success.

ACKNOWLEDGMENTS

I would thank M. Aotsuka and the Nogami family for their hospitality and logistical support on Teuri Island and Y. Nakayama for analyzing diet energy value. Thanks are also due to H. Mori and H. Abe for their encouragement throughout this study as part of my Ph.D. dissertation at the Institute of Applied Zoology, Hokkaido University. I am grateful to M. Fujioka, D. W. Mock, W. A. Montevecchi, K. Vermeer and A. Kato for their useful and critical comments on the various versions of the manuscript. This study was partly supported by a Fellowship for Young Scientists by the JSPS. The Agency for Cultural Affairs and Environment Agency gave permits to work on the island.

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