# ENERGY INTAKE, KLEPTOPARASITISM RISK, AND PREY CHOICE BY GLAUCOUS-WINGED GULLS (*LARUS GLAUCESCENS*) FORAGING ON SEA STARS

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ABSTRACT.—Energy gain is thought to play a central role in prey selection by most foragers, but it may conflict with food theft avoidance and be constrained by undeveloped foraging skills. We investigated predation by the Glaucous-winged Gull (*Larus glaucescens*) on the ecologically important Ochre Sea Star (*Pisaster ochraceus*). We tested the hypothesis that *Pisaster* size selection by gulls was based on energetic profitability, defined as energy provided per unit handling time. We then examined the degree to which profitability interacts with intraspecific kleptoparasitism risk and age-related foraging efficiency (i.e., energy intake rate, prey capture success) to produce the patterns of prey choice observed in a natural setting. Behavioral observations of free-living gulls revealed moderate to high (32.5–91.6%) occurrences of *Pisaster* in gull diets. We used handling time data and bomb calorimetry to determine the relationship between *Pisaster* size and energetic profitability, which informed prey offer experiments that allowed us to test hypotheses regarding gull prey choice. We found that gulls readily distinguished between *Pisaster* sizes on the basis of energetic profitability, selecting the most profitable individual in 60% of trials. Prey discrimination ability did not differ between gull age classes and thus did not contribute to the reported reduced foraging efficiency of juveniles. However, gulls exhibited a significant nonlinear decrease in preference for highly profitable *Pisaster* with increasing kleptoparasitism risk. *Received 13 May 2011, accepted 29 August 2011.*

Key words: age-related foraging efficiency, foraging behavior, Glaucous-winged Gull, intraspecific kleptoparasitism, *Larus glaucescens*, *Pisaster ochraceus*, prey choice decisions.

## Apport énergétique, risque de kleptoparasitisme et choix des proies par *Larus glaucescens* s'alimentant d'étoiles de mer

RÉSUMÉ.—Les gains énergétiques joueraient un rôle central dans la sélection des proies pour la plupart des individus, mais ils peuvent entrer en conflit avec l'évitement du vol de nourriture et être limités par des aptitudes peu développées pour la collecte de nourriture. Nous avons étudié la prédation par *Larus glaucescens* sur une espèce d'étoile de mer écologiquement importante, *Pisaster ochraceus*. Nous avons testé l'hypothèse que la sélection de la taille de *Pisaster* par les goélands était basée sur la rentabilité énergétique, qui est définie comme l'énergie fournie par unité de temps de manipulation. Nous avons ensuite examiné à quel degré cette rentabilité interagit avec le risque de kleptoparasitisme intraspécifique et l'efficacité de collecte de nourriture associée à l'âge (c'est-à-dire le taux d'ingestion d'énergie et le succès de capture des proies) afin de reproduire les patrons de sélection des proies observés dans un cadre naturel. Des observations comportementales de goélands en liberté ont révélé des occurrences de *Pisaster* dans le régime alimentaire des goélands allant de modérées à élevées (32,5–91,6 %). Nous avons utilisé les données de temps de manipulation et la bombe calorimétrique pour déterminer la relation entre la taille de *Pisaster* et la rentabilité énergétique, à partir d'expériences où des proies étaient offertes afin de tester les hypothèses concernant le choix des proies par les goélands. Nous avons trouvé que les goélands distinguaient facilement les tailles de *Pisaster* en se basant sur la rentabilité énergétique, puisqu'ils sélectionnaient les individus les plus profitables lors de 60 % des essais. La capacité de discriminer les proies n'était pas différente entre les classes d'âge des goélands et n'a donc pas contribué à l'efficacité réduite de collecte de nourriture rapportée chez les juvéniles. Cependant, les goélands ont montré une diminution non-linéaire significative de la préférence pour les individus de *Pisaster* hautement profitables avec un risque de kleptoparasitisme accru.

FORAGING THEORY SUGGESTS that an individual should discriminate between available prey types, consuming prey that yield the highest energy intake rate or lowest starvation risk (Stephens and Krebs 1986, Hamilton 2010). Energetic profitability, defined as the amount of energy provided by a prey item per unit of time required to capture and consume it (handling time), is considered an important criterion for judging the relative value of different prey types (Elner and Hughes 1978, Richardson and Verbeek 1986,

van der Steen 1999, Sih and Christensen 2001). However, prey choice may be subject to alternative dietary considerations (e.g., nutrient intake rate [Pulliam 1975], toxin avoidance [Belovsky and Schmitz 1994], or minimization of indigestible material [Bustnes and Erikstad 1990]), inability to distinguish the most valuable prey item (Draulans 1984, Ward 1991, Hamilton et al. 1999), and tradeoffs between prey quality and the risk of food theft (Hockey and Steele 1990, Langen and Rabenold 1994, Nilsson et al. 2000). Thus, it is often unclear to what extent foragers use information on relative prey value when selecting prey in complex field settings. Although selection of the most energetically profitable prey type suggests adherence to an optimal diet (Berec et al. 2003, Snellen et al. 2007), apparently suboptimal prey choices may not indicate a lack of support for the theory but rather the presence of an unmeasured factor affecting relative prey value (Sih and Christensen 2001).

One such factor, food theft (or kleptoparasitism), can be costly to the host individual in terms of energy and time spent searching for and handling prey items that are not ultimately consumed (Giraldeau and Caraco 2000). Additional costs are incurred by species in which kleptoparasitic attack results in energetically demanding high-speed aerial chases or potentially dangerous aggressive interactions, as is the case for gulls (family Laridae) and other sea birds (Brockmann and Barnard 1979, Burger and Gochfeld 1981, Gilardi 1994). In several species that forage in aggregations, and for which kleptoparasitic attacks are common, individuals have been shown to shift prey selection away from the most energetically profitable (and therefore most hotly contested) prey types in situations where the risk of food theft is high (Hockey and Steele 1990, Langen and Rabenold 1994, Nilsson et al. 2000). Thus, foragers may pay a cost in terms of energy intake rate, manifested as the selection of lower-quality prey, in order to reduce the risk of theft. This interaction between kleptoparasitism risk and prey choice is likely to be dependent on the local density of conspecifics and is applicable to intertidal foraging gulls, in which high rates of kleptoparasitism have consistently been documented (Barash et al. 1975, Rockwell 1982, Steele and Hockey 1995, Bertellotti and Yorio 2001, Galván 2003).

We examined predation by the Glaucous-winged Gull (*Larus glaucescens*; hereafter "gull") on the Ochre Sea Star (*Pisaster ochraceus*; hereafter *Pisaster*), two highly abundant species on the Pacific coast of North America. Previous studies on the diet of gulls have cited low occurrences of *Pisaster*—between zero and ~10% (Trapp 1979, Vermeer 1982, Murphy et al. 1984, Irons et al. 1986, Wootton 1997). However, our own observations suggest that *Pisaster* is a common prey item for gulls in rocky intertidal areas of southern British Columbia. *Pisaster* are always swallowed whole, resulting in exceptionally long handling times for large ones (up to ~45 min; J. P. Suraci pers. obs.). The broad range of *Pisaster* sizes (from <1 to >20 cm radius; Paine 1976, J. P. Suraci pers. obs.) that occurs at intertidal sites and the continuous range of energetic profitability values represented by these sizes may lead to difficulty in selecting the most valuable prey (Hughes 1979, Ward 1991), particularly for inexperienced foragers. There is a well-documented increase in foraging efficiency (i.e., energy intake rate, prey capture success) associated with gull age (Verbeek 1977, Searcy 1978, Burger and Gochfeld 1981, Greig et al. 1983, Skórka and Wójcik 2008), which is frequently attributed to learning required by juveniles to master complex foraging techniques (Searcy

1978, MacLean 1986, Marchetti and Price 1989, Forslund and Pärt 1995). The ability to discriminate between prey types on the basis of relative quality (e.g., energetic profitability) may be one of the skills that develops in juvenile gulls, a possibility that has not previously been addressed. *Pisaster* is an ecologically important intertidal predator—the original "keystone species" (Menge et al. 1994, Robles et al. 1995)—and gull prey choice when foraging on this sea star may therefore play an important role in structuring intertidal communities.

We used a combination of prey energy content analyses, field-based behavioral observations, and prey choice experiments to address the following questions: (1) Does *Pisaster* constitute a major prey species for gulls foraging in our study area? (2) Are gulls able to distinguish among *Pisaster* sizes on the basis of relative prey value? (3) Are differences in energetic profitability the main driver of prey choice? (4) Does the ability to discern the most valuable prey item differ between gull age classes? (5) Does kleptoparasitism risk affect the relative value of individual *Pisaster* and active size choice by gulls?

## Methods

*Behavioral field studies.*—Field work was conducted from April to September 2009 and April to August 2010 at two sites in southern British Columbia: Stanley Park (49°18′10″N, 123°7′35″W), ~2 km from downtown Vancouver, and Roberts Creek (49°25′48″N, 123°40′25″W), a partially wooded but largely residential area on the Strait of Georgia. Gulls and *Pisaster* were abundant at both sites, and preliminary observations suggested that *Pisaster* made up a substantial portion of the gull diet at these sites. Roberts Creek is a rocky intertidal habitat dominated by Rock Weed (*Fucus gardneri*), with considerable barnacle (*Semibalanus cariosus* and *Balanus glandula*) cover. Stanley Park has a mixed substrate consisting of mud and sand with small to medium sized boulders. This site is located on Burrard Inlet, a major shipping and recreational waterway for the city of Vancouver. Blue Mussels (*Mytilus edulis*) dominate the upper shore levels at Stanley Park and the lower intertidal zone is mainly covered by kelp (*Nereocystis luetkeana* and *Laminaria saccharina*). All field work was conducted from 2 h before to 2 h after daily low tide on days when the tidal minimum was ≤1.3 m. This range represents both the time of day and the tidal period when gull intertidal foraging and group size are at a maximum (Irons et al. 1986, J. P. Suraci pers. obs.), thereby reducing the likelihood of obtaining multiple measurements from single individuals. Daily foraging group size peaked, on average, at 37.2 gulls (peak range: 18–62) at Roberts Creek and 38.5 gulls (peak range: 19–65) at Stanley Park.

We conducted ~260 h of behavioral observations over the two field seasons. Data collection was conducted using a Canon high-definition digital camcorder (HDV 1080i). We performed focal animal sampling (Altman 1974) on randomly selected gulls foraging in the intertidal zone. Focal samples lasted for a maximum of 10 min or until the gull left the intertidal zone. These samples provided a continuous record of all behaviors and prey selections and were used to determine handling times for all common prey types. "Group videos" in which the foraging behavior of 2 to 10 gulls was recorded simultaneously were performed to increase the data-acquisition rate. Gulls in group videos were then "followed" individually during video analysis to obtain handling

time data. Opportunistic handling times from nonfocal gulls were also measured (to 0.1 s) using a stopwatch.

We analyzed all behavior video data digitally using Apple IMOVIE HD, version 6.0. Handling times, defined as the time between first contact with a prey item by a gull's beak and the resumption of search following prey consumption, were measured to the nearest 0.1 s. For each consumption event we noted time of day, tide level (in relation to lowest low tide for the site), and whether the gull was juvenile or adult on the basis of plumage. Juveniles were in their second, third, or fourth summer plumages (Howell and Dunn 2007). Because the study was conducted during the breeding season first-summer gulls were rare on the foraging grounds, and when they occurred (in mid- to late August) they were excluded from analyses.

We estimated *Pisaster* size in relation to gull beak length using video screen shots and the open-source image processing software IMAGEJ. We assumed an average gull beak length of 5.9 cm (James-Veitch and Booth 1954) and measured all *Pisaster* sizes as the length of the longest ray, essentially the radius of this radially symmetrical animal. We tested the validity of this method by measuring ray length (using measuring tape) of 58 *Pisaster* (0.8–6.7 cm radius) and then obtaining size estimates from video of gulls handling these sea stars. The average (± SD) of the absolute value of the difference between measured and estimated *Pisaster* size was 0.14 ± 0.10 cm (max difference = 0.4 cm). We found no significant difference between the measured and estimated values (one-way analysis of variance [ANOVA], $F = 0.001$, $P = 0.98$).

Gull fecal samples were analyzed for presence or absence of *Pisaster* ossicles (small bone-like structures that pass relatively intact through the gull digestive system). Fecal samples were randomly collected on 23 July and 8–11 August 2010 at Roberts Creek and on 24 July and 19 August 2010 at Stanley Park. Samples were collected in sterile plastic vials (50 mL Falcon tubes) and stored in 10% formalin at 4°C until analyzed.

Pisaster *energetic content.*—We used bomb calorimetry to estimate the energetic content of 33 *Pisaster* throughout the range of sizes consumed by gulls ("edible" size range: 0.8–8.6 cm, as observed in this study). *Pisaster* were collected during summer 2009 from both Roberts Creek and Stanley Park. On the day of collection, we measured the wet mass (to 0.01 g using an electronic balance) and ray length (to 0.1 cm) of each. *Pisaster* were then frozen at –20°C until needed. We homogenized individuals in a Waring blender and then lyophilized these homogenized samples to constant dry weight (~30% original wet mass). Caloric content was then determined for 1-g subsamples from each *Pisaster* using a Parr 1341 oxygen bomb calorimeter following the procedure outline in the manual (Parr Instrument Company, Moline, Illinois). The proportion of nonmetabolizable material for a given *Pisaster* size was estimated by taking the mass of calcareous material remaining after combustion of each homogenized subsample. This proportion remained relatively constant across *Pisaster* sizes at 16.28 ± 0.85 (SE) percent of *Pisaster* wet mass.

Prey *offer experiments.*—We conducted cafeteria-style prey offer experiments in the field from May to August 2010 to test the hypothesis that gulls select between *Pisaster* sizes on the basis of differences in energetic profitability. An experimental trial consisted of placing four *Pisaster* of different sizes in a tight circle

~30 cm in diameter on an exposed surface (e.g., rock or sand) in the intertidal zone. *Pisaster* were placed such that they would be simultaneously encountered by, and equally available to, a foraging gull. The four *Pisaster* size classes (SC) used in each trial were SC1 (arm length 0.5–1.9 cm), SC2 (2.0–3.5 cm), SC3 (4.0–5.5 cm), and SC4 (6.0–7.5 cm). These size classes were chosen such that (1) the edible range of sizes was well represented in each trial and (2) there was always one size class (SC2) that was distinctly more profitable than the others (see below). A trial began when a foraging gull encountered a prey offering. We recorded the age class of the individual (juvenile or adult), which sea star was selected first, the order of additional sea stars taken (if this occurred), and the number of other gulls within 5 m (as a proxy for kleptoparasitism risk).

## Statistical Analyses

*Classical tests.*—We used the Shapiro-Wilk test to test for normality of data. Data that passed this test were analyzed with one-way ANOVA. If the assumption of normality was not met we used the nonparametric Wilcoxon's rank sum test. Differences between proportional data were analyzed using chi-square tests when the number of observations in each category was >5. When this was not the case Fisher's exact test was used.

Pisaster *handling time model.*—We used a linear mixed effects model to analyze the relationship between handling time and *Pisaster* size (measured as length of the longest ray), setting individual gull as a random effect to account for multiple handling time observations taken from some individuals. Handling time data were natural log transformed to approximate a normal distribution and to correct for heteroscedasticity. Linear mixed effects models were fit using the lmer function from the package lme4 in R (R Development Core Team 2008). Because this function does not provide a measure of goodness-of-fit for the model, we report a pseudo-$R^2$ value, calculated as the square of the correlation between the predicted values from the model and the values of the response variable (Draper and Smith 1981). The decision to not include other covariates for which we have data in the handling time model was made because we were interested in assessing the relationship between handling time and size as generalized across sites, gull age classes, and tide levels. Predictions from this model were used in generating energetic profitability estimates for all relevant *Pisaster* sizes, which we wished to be applicable over a range of conditions.

Pisaster *energy content model.*—We used standard linear regression analysis to determine the relationship between *Pisaster* size and energy content. Both variables, energy (in kilojoules) and size, were natural log transformed. Estimates from the energy content and handling time models were used to determine energetic profitability for relevant *Pisaster* sizes. Error from both models was incorporated into error estimates for energetic profitability using delta method variance approximation (Powell 2007).

*Prey offer experiments.*—Chi-square tests were used to compare selection frequencies of the four *Pisaster* size classes. We were also interested in whether a particular size class was selected more or less frequently than would be expected by chance alone; our null expectation in this analysis was that size classes should be selected in accordance with their proportional abundance in each trial of 25%.

We used logistic regression (generalized linear model with binomial distribution) and stepwise model selection to evaluate several factors with potential effects on *Pisaster* size choice. The response variable in these models was a binomial variable describing

whether the most profitable *Pisaster* (SC2) was selected first (1 = yes, 0 = no). Explanatory variables tested included (1) site—Stanley Park or Roberts Creek, (2) age of the focal gull—juvenile or adult, (3) kleptoparasitism risk—number of conspecifics within 5 m, and (4) length of time from daily tidal minimum (range: 0.03–2.17 h). The last measure was chosen in place of a direct measurement of tide level to facilitate comparison across sites because the magnitude of tidal flux during our observation periods differed between the two sites (Roberts Creek, range: 0.1–1.8 m; Stanley Park, range: 0.3–1.6 m). Beginning with a full model that included all of the above terms plus the interaction between kleptoparasitism risk and time from tidal minimum we followed the stepwise model selection procedure outlined by Zuur et al. (2009). Data from all 75 trials were used and models were fit using the glm function in R.

We predicted that the probability of selecting the most profitable *Pisaster* first in our prey offer experiments would decline with increasing kleptoparasitism risk. Our most profitable *Pisaster* size class (SC2) required a longer handling time than SC1, the smallest size class, and therefore allowed a greater opportunity for theft by kleptoparasites. We hypothesized that as the number of potential kleptoparasites in proximity to the focal gull increased, the gull's probability of selecting the most energetically profitable *Pisaster* over the most quickly consumed would decrease. We used logistic regression to test this hypothesis, setting the probability of selecting the most profitable *Pisaster* as the response variable and the number of conspecifics within 5 m of the focal gull as the explanatory variable. For this analysis we were only interested in trials in which either SC2 (the most profitable size class) or SC1 (the most quickly consumed size class) was selected first (*n* = 70). All trials in which this was not the case (*n* = 5) were dropped from the analysis. To test the significance of our kleptoparasitism risk model we performed a likelihood ratio test (with a chi-square distribution) on the difference in explained (or residual) deviance between this model and a null model with no predictors (Hosmer and Lemeshow 2000). The chi-square statistic in this test is the difference in residual deviance and the degree of freedom is the difference in degrees of freedom between the two models.

### Results

Our field observations showed that the diversity of prey types exploited by gulls and the degree to which gulls relied on *Pisaster* varied greatly between the two field sites. At Roberts Creek *Pisaster* was the dominant prey type by far; of a total of 322 observed prey consumptions, 91.6% (*n* = 295) were *Pisaster*. This predominantly sea star diet was supplemented by polychaete worms (*Nereis* spp.; 3.1%) and a set of small invertebrates (5.3%) that consisted mainly of several species of gastropod as well as hermit crabs. At Stanley Park, *Pisaster* made up a significantly smaller proportion of the observed prey consumptions ($\chi^2$ = 279.5, df = 1, *P* < 0. 001). Of 526 observed prey consumptions, 32.5% (*n* = 171) were *Pisaster*. Other major prey types at this site include Nuttall's Cockles (*Clinocardium nuttallii*), crabs (*Cancer productus* and *C. magister*), polychaete worms, Blue Mussels (*Mytilus trossulus*), Green Sea Urchins (*Strongylocentrotus droebachiensis*), and a "small invertebrate group" similar to the one described for Roberts Creek.

Random samples of gull feces collected at the two sites provided an additional measure of the occurrence of *Pisaster* in gull diets. At Roberts Creek, 90.0% of fecal samples (45 of 50) contained *Pisaster* ossicles, whereas only 12.5% (6 of 48) contained ossicles at Stanley Park. This difference was again significant ($\chi^2$ = 55.87, df = 1, *P* < 0.001).

*Pisaster* *profitability estimates.*—Handling times were recorded for a total of 223 *Pisaster* consumptions, observed at both sites over the two field seasons. Gulls at our sites consumed *Pisaster* individuals that were 0.8–8.6 cm in radius. Our linear mixed effects model showed a strong positive relationship between *Pisaster* size and gull handling time ($T_H$) ($R^2$ = 0.87; Fig. 1) and produced the following regression equation:

$$\ln T_H \,(s) = -0.17 + 0.93 * \text{size (cm)} \tag{1}$$

The 95% confidence limit (CL) for the slope (0.93 ± 0.08) did not cross zero, which lends additional support to the significance of this relationship.

As expected, there was a strong positive relationship between *Pisaster* energy content (*E*) and body size ($R^2$ = 0.97, *P* < 0.001; Fig. 2):

$$\ln E \,(kJ) = 0.33 + 2.55 * \ln \text{size (cm)} \tag{2}$$

The parameter estimate for the slope was also significant (slope ± 95% CL = 2.55 ± 0.16, *P* < 0.001).

Energetic profitability ($E/T_H$, calculated by taking the quotient of Equation 2 and Equation 1 for all relevant *Pisaster* sizes) was a peaked function of *Pisaster* size (Fig. 3) that reached a maximum of 1.67 kJ s$^{-1}$ for 2.7-cm sea stars. Profitability declined quickly with
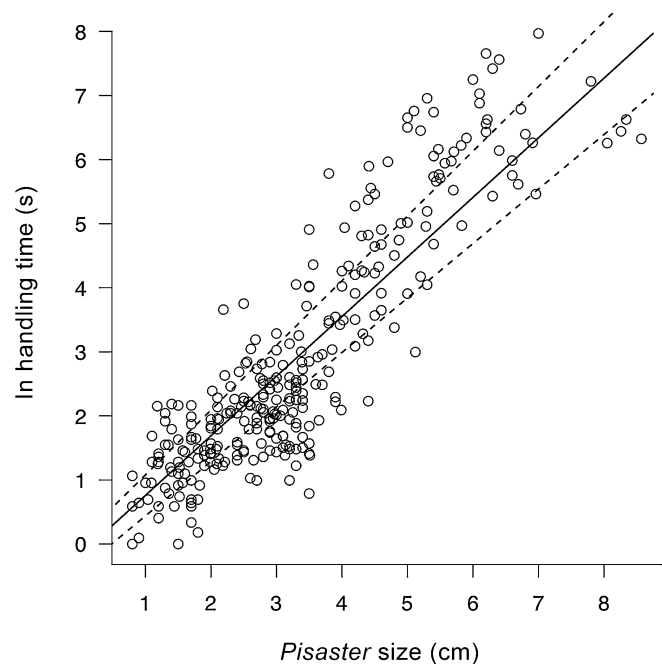


FIG. 1. Relationship between *Pisaster* size (measured as longest ray length) and gull handling time as fit by linear mixed-effects model. Handling time of Glaucous-winged Gulls has been natural log transformed to normalize the data. Dashed lines are 95% confidence intervals around model fit.
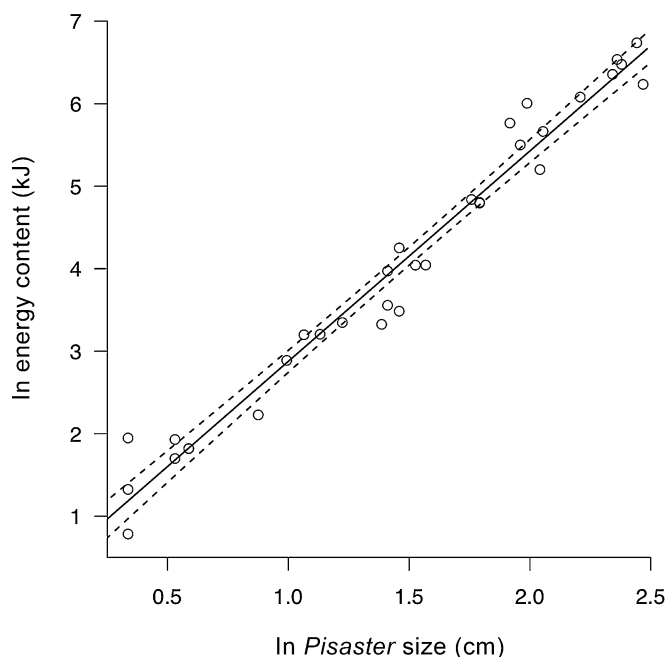
FIG. 2. Relationship between *Pisaster* size (longest ray length) and energy content of the whole individual as fit by linear regression. Both variables have been natural log transformed to normalize the data. Dashed lines are 95% confidence intervals.



FIG. 3. Estimated energetic profitability (kJ s$^{-1}$) for *Pisaster* sizes (longest ray length) throughout the range of sizes consumed by Glaucous-winged Gulls. Estimates were derived by taking the quotient of predictions from the *Pisaster* energy content regression and the handling time mixed model (see text). Dashed lines are 95% confidence intervals around mean energetic profitability determined using the delta variance approximation method.

increasing size and reached a minimum of 0.13 kJ s$^{-1}$ for the largest sea star taken by a gull in this study (size = 8.6 cm radius).

*Prey offer experiments.*—The most profitable size class, SC2, was selected first by foraging gulls in 60.0% of trials (45 of 75 trials; Fig. 4). This was significantly greater than SC1 (33.3%; $\chi^2 = 9.67$, df = 1, $P = 0.002$), SC3 (6.7%; $\chi^2 = 45.63$, df = 1, $P < 0.001$), SC4 (0%; $\chi^2 = 61.46$, df = 1, $P < 0.001$), and all three other size classes combined (40.0%; $\chi^2 = 5.23$, df = 1, $P = 0.022$).

Our results suggest that gulls select sea stars in relation to their energetic profitability. SC2 (mean profitability ± SE of all *Pisaster* offered = 1.62 ± 0.01 kJ s$^{-1}$) was selected significantly more frequently than would be expected on the basis of its 25% proportional availability ($\chi^2 = 17.39$, df = 1, $P < 0.001$; Fig. 4). The selection frequency of SC1 (profitability ± SE = 1.03 ± 0.03 kJ s$^{-1}$) was not significantly different from the null expectation of 25% ($\chi^2 = 0.90$, df = 1, $P = 0.35$), whereas both SC3 (profitability ± SE = 1.00 ± 0.01 kJ s$^{-1}$) and SC4 (profitability ± SE = 0.42 ± 0.01 kJ s$^{-1}$) were selected significantly less frequently than expected on the basis of proportional availability (SC3: $\chi^2 = 8.13$, df = 1, $P = 0.004$; SC4: $\chi^2 = 19.20$, df = 1, $P < 0.001$).

For trials in which SC2 was chosen first and the focal gull chose a second *Pisaster* ($n = 32$), SC1 was chosen second (75% of trials) significantly more often than SC3 (25% of trials; $\chi^2 = 14.06$, df = 1, $P < 0.001$). In total, there were 25 trials in which SC2 was not chosen first and a second *Pisaster* was chosen. In these 25 trials SC2 was selected as the second *Pisaster* (24 trials, 96%) significantly more often than SC1 (1 trial, 4%; $\chi^2 = 38.72$, df = 1, $P < 0.001$).

In our logistic regression analysis of several factors with potential effects on *Pisaster* size choice the only model term that, when dropped, resulted i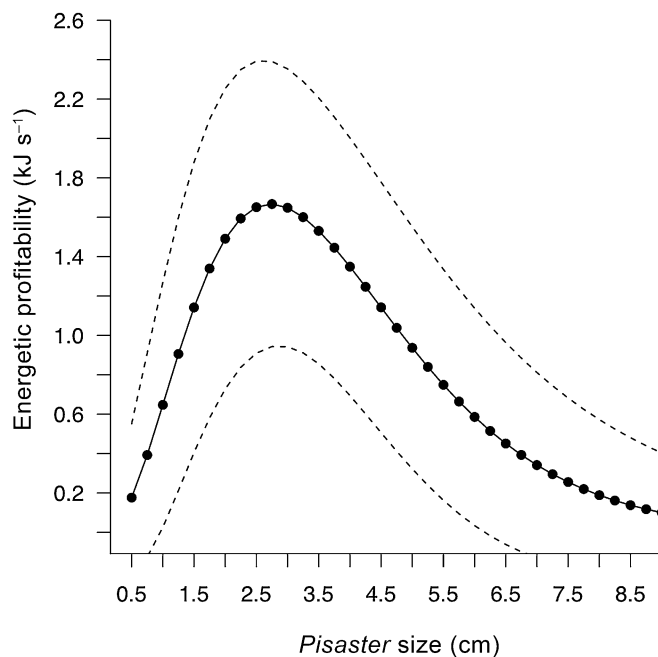n a significant decrease in explained deviance—as determined by likelihood ratio tests (LRT)—was the number of conspecifics within 5 m ($\chi^2 = 18.10$, df = 1, $P < 0.001$). The terms for site, age of focal gull, time from daily low tide, and the interaction between number of conspecifics and time from low tide were all nonsignificant (all LRT $P$ values ≥ 0.1) and were excluded from the best model based on stepwise model selection (Zuur et al. 2009).

The lack of an effect of both site and gull age on the probability of selecting the most profitable *Pisaster* first was confirmed by chi-square tests. At Stanley Park, SC2 was selected first in 60.6% of trials (20 of 33), which was not significantly different from Roberts Creek, where SC2 was selected first in 59.5% of trials (25 of 42; $\chi^2 = 0$, df = 1, $P = 1$). Adult gulls selected SC2 first in 59.0% of trials (23 of 39), compared to 61.1% for juveniles (22 of 36 trials; $\chi^2 = 0$, df = 1, $P = 1$). When we excluded trials in which the number of gulls within 5 m was greater than zero and, thus, removed the effect of kleptoparasitism, the proportion of trials in which SC2 was selected first increased to 80.0% for adults and 93.3% for juveniles. This difference was again nonsignificant (Fisher's exact test, odds ratio = 0.29, $P = 0.365$).

Logistic regression showed a significant negative relationship between the number of conspecifics in proximity to a focal gull (i.e., level of kleptoparasitism risk) and the gull's probability of selecting the most profitable *Pisaster* (SC2) over the most quickly consumed (SC1; Fig. 5). Both the slope and intercept of this model were significant (intercept: $P < 0.001$, slope: $P = 0.002$), as was the amount of deviance explained by the model (likelihood ratio test between residual
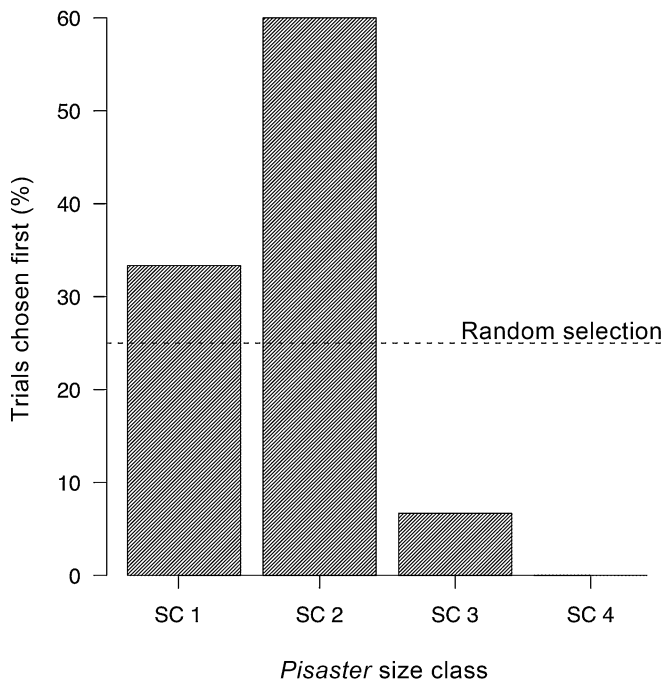
FIG. 4. Percentage of total prey offer trials in which each *Pisaster* size class was selected first by Glaucous-winged Gulls in British Columbia in 2009 and 2010. The four *Pisaster* size classes used in each trial were SC1 (arm length = 0.5–1.9 cm), SC2 (2.0–3.5 cm), SC3 (4.0–5.5 cm), and SC4 (6.0–7.5 cm). The dashed line represents the null hypothesis of random selection.
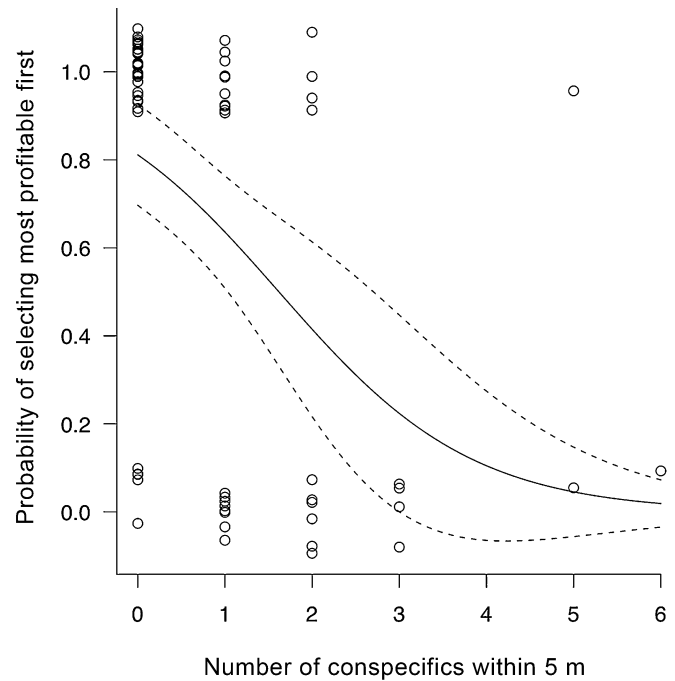


FIG. 5. The probability that a Glaucous-winged Gull in British Columbia selected the most energetically profitable *Pisaster* in a prey offer trial when the number of other gulls within 5 m ranged from 0 to 6 birds. Points correspond to individual trials in which the focal gull either selected the most profitable *Pisaster* (1) or the smallest, most quickly consumed *Pisaster* (0). A small amount of random noise has been added to the data to differentiate individual data points. The solid line represents predictions from a logistic regression model regarding the change in the probability of a gull selecting the most energetically profitable *Pisaster* over the most quickly consumed as number of conspecifics (and, therefore, kleptoparasitism risk) increases. The dashed lines are 95% confidence intervals around probability predictions.

and null deviance: $\chi^2 = 14.99$, df $= 1$, $P < 0.001$). According to the model the probability ($\pm$ 95% CL) of a gull selecting the most profitable sea star first declined from 81.1 $\pm$ 11.5% when no other gulls were within 5 m to 1.9 $\pm$ 5.4% when 6 gulls were in proximity (the maximum number of conspecifics we observed in our trials; see Fig. 5).

## Discussion

*Occurrence of sea stars in the gull diet.*—Previous studies have found that sea stars, including *Pisaster*, comprise 0–10% of gull diets in the Northeastern Pacific, which suggests that sea stars are not major prey types for gulls (Trapp 1979, Vermeer 1982, Irons et al. 1986, Wootton 1997, Snellen et al. 2007). Our study, however, shows that *Pisaster* is in fact an extremely common prey species, constituting >90% of the prey items consumed by Glaucous-winged Gulls at at least one intertidal site. Whether this difference is because of site selection, sampling method, or an actual change in the use of sea stars as prey over the past three decades is unknown. *Pisaster* is often considered a top predator in intertidal food webs (e.g., Navarrete et al. 2000), a conception that is clearly inconsistent with our findings.

That *Pisaster* constitutes a major gull prey species is perhaps unsurprising because calculations of energetic profitability for this species, which range from 0.13 to 1.67 kJ s$^{-1}$, are comparable to those reported for other major gull prey types. Irons et al. (1986) found that the most profitable prey type taken by Glaucous-winged Gulls at intertidal sites in the Rat Islands, Alaska (the chiton *Katharina tunicata*), provided an energetic return of 2.06 kJ s$^{-1}$. Snellen

et al. (2007), studying Western Gulls (*Larus occidentalis*), a closely related species (Chu 1998), found that the most energetically profitable size of Purple Sea Urchin (*Strongylocentrotus purpuratus*) taken at a coastal site in southern California provided 0.48 kJ s$^{-1}$.

*Optimal size choice and age effects.*—The ability of a forager to discriminate between prey sizes on the basis of energetic profitability (or any other currency that scales with body size; e.g., nutrient or protein content) is key to choosing an optimal diet (Ward 1991, Hamilton et al. 1999). However, theoretical work on foragers in general (Hughes 1979) and empirical work on birds in particular (Draulans 1984, Ward 1991, Hamilton et al. 1999) suggests that for many species the ability to distinguish between prey types or between sizes of a single prey species may be imperfect, leading to "suboptimal" prey selection. Our results indicate that Glaucous-winged Gulls readily discriminate between *Pisaster* sizes on the basis of energetic profitability and that profitability plays a primary role in driving size choice. Foraging efficiency (i.e., energy intake rate, prey capture success) has consistently been found to increase with gull age (Verbeek 1977, Searcy 1978, Burger and Gochfeld 1981, Greig et al. 1983, Skórka and Wójcik 2008). However, we found no difference between juveniles and adults in the probability of selecting the most profitable size class in our prey

offer trials. Both age classes chose SC2 in ~60% of trials, and this proportion increased (to 80.0% for adults and 93.3% for juveniles) when no other gulls were in proximity to the prey choice experiment. This suggests that the discrepancy in foraging efficiency between juveniles and adults is not due to differential prey-recognition ability in this species, a novel finding given that previous studies have concentrated on age differences in the ability to capture and consume prey rather than the ability to discern the most profitable prey types (Verbeek 1977, Searcy 1978, Burger and Gochfeld 1981, Greig et al. 1983, MacLean 1986, Skórka and Wójcik 2008; but see Snellen et al. 2007).

*Kleptoparasitism risk and optimal size choice.*—Our results indicate that the likelihood of successfully consuming the smallest *Pisaster* must be greater than that of consuming the most profitable *Pisaster* when the risk of food theft or displacement by other gulls is high. Also, the greater probability of successful consumption associated with small *Pisaster* must progressively outweigh the cost of an energetically suboptimal prey selection (profitability cost = 1.62 kJ s$^{-1}$ [best *Pisaster*] − 1.03 kJ s$^{-1}$ [smallest *Pisaster*] = 0.59 kJ s$^{-1}$) as the number of conspecifics increases.

High rates of intraspecific kleptoparasitism are well documented among the Laridae (Brockman and Barnard 1979, Burger and Gochfeld 1981, Steele and Hockey 1995, Bertellotti and Yorio 2001, Galván 2003), and *L. glaucescens* is no exception (Barash et al. 1975, Rockwell 1982). Previous work on a range of taxa (Rockwell 1982, Ens et al. 1990, Steele and Hockey 1995, Nilsson et al. 2000, Bertellotti and Yorio 2001) has shown that kleptoparasitic individuals preferentially target hosts with larger prey items because this increases both probability of success (Rockwell 1982, Steele and Hockey 1995) and energetic return (Thompson 1986). Potential hosts, in turn, have been shown to switch their foraging preferences toward smaller, less energetically profitable prey items in situations where kleptoparasitism risk is high (Thompson and Barnard 1984, Hockey and Steele 1990, Nilsson and Brönmark 1999, Snellen et al. 2007). Our results are consistent with these findings and suggest that kleptoparasitism will have a substantial effect on *Pisaster* size selection by naturally foraging gulls in southern British Columbia, where site-level group sizes commonly exceed 40 individuals (present study).

Selection of the most profitable *Pisaster* was not perfect even when the effect of kleptoparasitism risk was removed (gulls selected SC2 in 87.5% of prey offer trials with no conspecifics present). Whether this results from perceptual errors in distinguishing prey items or an additional unmeasured variable affecting size preference is unknown.

Both profitability and kleptoparasitism risk appear to play key roles in *Pisaster* size selection by gulls, which illustrates the importance of the interaction between these two factors in determining resource use in this system. Our findings may prove useful to future studies of Pacific intertidal community ecology because the details of predator foraging decisions are known to have a substantial influence on prey population dynamics (Holt and Kimbrell 2007). The high rates of *Pisaster* consumption observed in this study and the ecological importance of *Pisaster* in shaping intertidal community structure warrant further investigation of this predator–prey interaction.

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