Oecologia (1994) 100:54–65

© Springer Verlag 1994

ORIGINAL PAPER

S.R. Beissinger · T.J. Donnay · R. Walton

Experimental analysis of diet specialization in the snail kite: the role of behavioral conservatism

Received: 2 July 1993 / Accepted: 3 July 1994

Abstract We examined factors maintaining extreme diet specialization in the snail kite *(Rostrhamus sociabilis),* a medium-sized hawk which feed almost exclusively on *Pomacea* snails, by determining why during some months kites eat crabs *(Dilocarcinus dentatus)* in the llanos of Venezuela. We offered snails and crabs of different sizes to wild free-flying birds to develop estimates for a prey choice model. Handling times of *Pomacea doliodes* snails averaged 90±39 s and were positively correlated with snail size. Handling times for crabs ($\bar{x}$=353±130 s) were significantly longer and exhibited greater variation than for snails, and were not correlated with crab size. Edible crab tissues had greater dry weights and contained more energy (25.37 kJ/g) than tissues of snails (16.91 kJ/g). Total energy of crabs was much greater than that of snails, and total energy of both foods was highly related to body length. We constructed an allometric equation for profitability of snails and crabs. Snails were more profitable than all but the largest crabs, but estimates of variance in profitability were greater for crabs. Predictions from the model were tested by offering crabs that represented equal, greater and much greater profitability than snails, to determine whether kites chose prey according to profitability. Only 15.6% of 289 food items chosen were crabs. Half of the 18 kites tested did not eat crabs and only 3 birds switched from snails to more profitable crabs. Four fledglings showed no preference for snails. The role of neophobia in food choice was investigated by offering unfamiliar snails *(Pomacea urceus)* to kites. Kites exhibited neophobic behaviors, and 5 of 12 birds chose not to capture *P. urceus*. Two-thirds of the 12 snails chosen were rejected immediately, but the others were handled efficiently ($\bar{x}$=133±89 s). Although morphological adaptations allow kites to specialize on snails, the costs of specialization were overcome for kites when the profitability of alternative food increased sufficiently. Our results suggest a role for behavioral conservatism, in the form of risk-averse foraging and neophobia, in maintaining severe diet specialization in the snail kite.

Key words Behavioral conservatism · Cost of specialization · Diet specialist · Profitability · Risk-averse foraging

Introduction

Optimal foraging theory predicts that the diet of predators should be composed of food items that maximize long-term average energy or nutrient intake, or minimize the risk of starvation or predation (Schoener 1971; Pyke 1984; Stephens and Krebs 1986). The decision to include a potential prey item in the optimal diet depends on the current physiological state of the forager (Caraco 1981; Richards 1983), and on the time and energy costs to capture and consume the food item, the energy and nutrient benefits obtained, and the predation risk compared to other potential food items available (Pyke et al. 1977; Krebs 1980; Sih 1980; Stephens and Krebs 1986). Under some circumstances, foragers are concerned not only with maximizing net energy intake per unit time (Schoener 1971), but also avoiding starvation and minimizing the variance in energy intake – so called "risk-sensitive foraging" (Caraco et al. 1980; Real and Caraco 1986). However, foraging success of predators is often constrained by a variety of factors that decrease encounters with profitable prey: food resources may exhibit temporal or seasonal fluctuations in abundance, predation pressure leads to selection of predation-avoidance behavior or adaptations by prey, and most environments are sufficiently complex to permit prey to hide or escape from

---

S.R. Beissinger (✉) · T.J. Donnay
School of Forestry and Environmental Studies, Yale University,
205 Prospect St., New Haven, CT 06511, USA

S.R. Beissinger
Department of Zoological Research, National Zoological Park,
Washington, DC 20008, USA

R. Walton
National Environmental Research Park,
Fermi National Accelerator Laboratory, Box 500,
Batavia, IL 60510, USA

predators. Thus, it is not surprising that diets of most predators are not composed exclusively of the most profitable food item but include a variety of different foods (Martin et al. 1951).

Animals that eat only one or two kinds of foods are rare among vertebrates, although invertebrate diet specialists are more common (Strong et al. 1984). Vertebrate diet specialists often have trophic appendages that are adapted for efficient processing of their preferred foods. Such morphological specialization is thought to carry a cost in the form of a decrease in efficiency when processing alternative foods (Levins 1968; Schoener 1971; MacArthur 1972). This cost of specialization has been suggested to reinforce diet specialization in vertebrate predators (Partridge and Green 1987; Benkman 1988; Meyer 1989), and is fundamental to nearly all models of specialization (Levins 1968; Futuyma and Moreno 1988).

Diet specialization is likely to lead to selection for particular kinds of foraging behaviors, since "behavior is often the mechanism by which specialization is exercised" (Futuyma and Moreno 1988). Often there is a "psychological" basis of specialization expressed as a neophobia or fear of new situations. This results in specialized foragers ignoring potential food items or foraging sites in favor of familiar ones (Coppinger 1969, 1970; Greenberg 1983, 1985). Likewise, generalists may form a search image that acts as a temporary psychological mechanism for specialization (Tinbergen 1960; but see Guilford and Dawkins 1987). Thus, it is not clear whether vertebrate diet specialization is a result of predatory behavior maintained by the costs of specialization, by behavioral sterotypy (Klopfer 1967), or by some combination of these forces.

We investigated the roles of profitability, risk and neophobia in prey choice by an extreme diet specialist, the snail kite *(Rostrhamus sociabilis).* This medium-sized hawk hunts in wetlands and feeds almost exclusively on one genus *(Pomacea)* of freshwater apple snails (Howell 1932; Snyder and Snyder 1969; Beissinger et al. 1988). Snail kites possess a long, slender, decurved bill that is adapted for extracting the body of a snail from its shell. The bill permits kites to cut the collumelar muscle attachment inside the first whorl of a snail's shell (Snyder and Snyder 1969; Voous and van Dijk 1973; Snyder and Kale 1983). The kite's bill morphology is much more strongly specialized for extracting snails than the bill morphology of other birds which eat snails as well as other food items (Snyder and Snyder 1969). Because of its trophic morphology, the snail kite might be expected to exhibit a cost of specialization when feeding on alternative foods.

Throughout most of its range, snail kites usually take alternative foods only when apple snails are unavailable. In Florida, the kite's diet is restricted to one species of snail *(Pomacea paludosa)* and only rarely have they been observed to eat other foods (small turtles, rats and other species of snails), mainly when apple snails were scarce during severe droughts or cold weather (Sykes and Kale 1974; Woodin and Woodin 1981; Beissinger et al. 1988, 1990a). Kites eat several species of *Pomacea* snails in Central and South America (Harverschmidt 1962, 1970; Weller 1967; Beissinger 1983; Snyder and Kale 1983), and upon occasion have eaten *Marisa* snails (Snyder and Kale 1983; Alves de Magalhães 1990).

Only in the llanos of Venezuela have snail kites been regularly observed to eat food other than apple snails (Mader 1981). Here snails *(Pomacea doliodes)* composed over 90% of the diet and freshwater crabs *(Dilocarcinus dentatus)* comprised the remainder (Beissinger 1990a). To consume crabs, kites quickly removed the abdomen, sometimes discarded the legs or claws, and spent long periods of time removing and eating very small bits of meat and organs from the exoskeleton (Beissinger 1990a). Crabs appeared unable to injure kites with their claws.

It is not clear why snail kites included crabs in their diet. Crabs were eaten primarily on a seasonal basis. They were rarely eaten in July and August, but increased to as much as 37% of the diet in September and October (Beissinger 1990a), when crabs had grown to their maximum size (Donnay and Beissinger 1993). Snails and crabs inhabit the same seasonal and permanent wetlands at similar, albeit variable, densities (Donnay and Beissinger 1993), so both should be encountered by foraging kites. But in some years snail abundance declined after August (Donnay and Beissinger 1993) and this might account for the increased occurrence of crabs in the diet of kites. On the other hand, kites might prefer crabs to snails, even though crabs require more time to eat (Beissinger 1990a), because crabs are larger and perhaps more profitable.

In this paper we analyze the factors maintaining diet specialization in the snail kite by experimentally examining why kites choose to include crabs in their diet. Food choice experiments were conducted with wild free-flying birds to estimate parameters for a prey choice model of profitability and risk for snails and crabs of different sizes. Predictions from the model were tested with wild free-flying kites by conducting behavioral titrations – dichotomous tests designed to examine the trade-offs in profitability between foods using snails and crabs of different sizes. Finally, the role of neophobia in food choice by kites was investigated by offering a congeneric snail species that kites have not been known to eat.

Material and methods

Field studies were conducted in the llanos of Venezuela at the ranch Hato Masaguaral (8° 34′ N, 67° 35′ W), 45 km south of Calabozo in the state of Guarico, and on other ranches along the main highway 30 km to the north and 80 km to the south. Descriptions of the area and climatological conditions are available in Eisenberg (1979), Beissinger et al. (1988), and O'Connell (1989).

Our studies were conducted with wild free-flying snail kites in their natural environment. They were induced to hunt from a perch and choose food from feeding trays described below. The experimental set-up mimicked one of the two dominant modes of foraging ("still-hunging") used by kites (Beissinger 1983): individuals land on a perch 2 m above the water, sit and wait, and then pounce on a desirable prey. When still-hunting, kites may encounter prey items simultaneously and/or sequentially.

All kites were completely unrestrained and their behavior was uncontrolled. During these studies, individual kites fed mostly from the trays, but sometimes captured snails or crabs away from the experimental set-up or used the perches intermittently. We assumed that all adult kites had been exposed to both food types prior to our study, which is likely to be true for most birds (Beissinger 1990a, 1990b; Donnay and Beissinger 1993). Because we used free-flying birds, we were unable to control for their state of hunger, except by restricting our experiments to the morning and late afternoon hours, which are the periods when kites forage most actively (Beissinger 1983). Individuals were identified by a combination of geographic location, plumage differences, and behavior patterns. Kites hunt solitarily, and in nearly all cases only one kite fed from the feeding trays. Although they do not defend all-purpose territories, kites sometimes defend rich patches of snails (Snyder and Snyder 1970) and defended the feeding trays during occasional visits by other kites.

Field trials

Field trials were conducted from July through November 1988 to estimate parameters for a model of profitability for snails and crabs of various sizes. Free-flying adult snail kites were provided with two floating 80×80×15 cm trays positioned on either side and in front of a perch, and filled with 8–10 cm of clear water and either snails or crabs of various sizes (after R. Chandler, personal communication; Bourne 1985a). The sides of the trays slanted at an angle of approximately 100° for kites to view clearly all prey items in the trays when looking down from above. We randomly chose trays in which to place the crabs and snails for a bird's first trial, and then alternated thereafter. Each food item was individually marked and measured (snail shell length and crab carapace length in mm) prior to placement in the trays. Length was used as an estimator of size because it could be easily determined from both living and dead animals, was more highly related to dry weight than either width or wet weight, and was the dimension used by the birds to grip crabs with their talons during capture. Sizes of snails (30–70 mm) and crabs (24–45 mm) offered to kites were determined from the range of food items recovered from beneath kite feeding perches. Although the range of lengths for crabs was smaller than for snails, crabs were actually larger than most snails because they were wider.

Fourteen individually identifiable kites were separately allowed to feed from the trays, each containing 5–10 food items, for up to 3 days. The food items chosen and the time required to eat them after perching (handling time) were recorded, the latter measured to the nearest second. When possible, we timed the components of the handling process for snails to determine which was the most time-consuming (Snyder and Snyder 1969): removing the snail's operculum, extracting the snail's body from its shell, or eating the body. No consistent, equivalent handling processes were distinguishable for crabs because the steps to process them were inconsistent and different (Beissinger 1990a). The identity of a chosen food item was determined by either observing its number using a 15–60 x spotting scope while it was being eaten, retrieving its discarded shell after it had been eaten, or checking the trays to determine which food item was missing. We also recorded whether the kite consumed each food item wholly or partially, fed it to its young or mate, or dropped it.

Allometric model of profitability for snails and crabs

We modeled profitability of snails and crabs of different sizes by developing allometric relationships for energy content and handling time for each food type from data collected during field trials. Profitability of a food item was defined as its total energy content [dry weight (g) × energy/g] divided by its handling time. Dry weights of snails and crabs were obtained by extracting the body tissues that kites normally consume and drying them at 50° C until weights had stabilized. Kites completely consumed snails, except for parts of the digestive and reproductive tracts, whereas only the soft parts in the crab's body cavity were ingested and the legs and claws were never eaten (Snyder and Snyder 1969; Beissinger 1990a). Estimating energy value of crabs by recovering eaten prey and determining the remaining energy would have greatly overestimated energy intake because kites ripped uneaten parts into many small pieces that were impossible to recover. Energy content was determined by bomb calorimetry for snail tissue by Beissinger (1983) and for crab tissue by Lancaster Laboratories, Lancaster, Pennsylvania.

We defined handling time as the time required to open and completely eat a food item after perching with it. We did not include the time required to find and capture the prey (search and pursuit time) or to fly with the food item to a perch after capture (returning time), although such costs are sometimes included in diet choice models (Stephens and Krebs 1986). The use of feeding trays standardized prey availability, so that search and pursuit time was limited to a pounce from the perch for both snails and crabs. Returning time is usually a minor component of a foraging bout (Beissinger 1983) and was not influenced by food type, but varied considerably among experimental locales, because it was affected by the distance from feeding trays to extraction perches (unpublished data). Since the goal of our model was to determine the energetic costs and benefits inherent to eating snails and crabs of different sizes, and our behavioral titration experiments controlled prey availability but not other environmental variables, we excluded search, pursuit and returning times from our measure of profitability. Inclusion of these time components would change the absolute values of profitability of snails and crabs slightly (since in our experiment search and pursuit costs were trivial relative to handling time) and introduce uncontrolled variation, but would not alter the predictions of which food items should be chosen in the behavioral titration experiment.

Allometric relationships between snail or crab body length, and dry weight, total energy content or handling time were determined by linear regression and inspection of residual plots using SYSTAT (Wilkinson 1990). To develop the best predictive allometric models, we examined linear, semilog, and log-log functions (Schoener 1979). While all fit the data well, we chose to employ the model with the highest r^2 value that best met the assumptions of normality for the dependent and independent variables and the residuals, paying particular attention to the upper and lower end of the range of lengths as their values played an important role in subsequent experiments. Profitability was estimated by evaluating total energy and handling time from the allometric equations for snails and crabs of various sizes. For the regression of handling time versus snail length, 3 of the 169 observations were considered outliers and were eliminated, because the handling times were extremely long (200–250 s) and they had an undue effect on the regression coefficients as tested by Cook's D (Wilkinson 1990).

An estimate of the variance of profitability was calculated in two steps. First, we estimated the variance in total energy or handling time associated with a particular length (L) of snail or crab. In this procedure, statistics from the regression of length versus total energy or handling time were used to derive estimates of probable values for new cases of total energy or handling time for a given length, and the variance applicable to such a forecast. Such a variance is called a "forecast" because it predicts a likely distribution of a dependent variable based on its relation to an independent variable (Ezekiel and Fox 1963). It is also known as the "tolerance limits" of a regression equation. The variance of the forecast is concerned with possible differences between estimated values (derived from the regression) and actual values for new observations. The individual forecast of energy and handling time was calculated for snails and crabs of length L from statistics derived from regression equations using the formula of Ezekiel and Fox (1963):

$$(s^2)_{\mathrm{L}} = \mathrm{MSE} + \mathrm{MSE}/n + s_{\mathrm{b}}^2 * (\overline{\mathrm{L}} - \mathrm{L})^2$$

where MSE is the residual mean square error, n is the sample size, s_{b} is the standard error of the regression coefficient, and $\overline{L}$ is the mean size. The second step in this procedure used these estimates of variance for energy and handling time in a Monte Carlo simulation. We generated a distribution of the profitability of 1000 snails and crabs of a given length from which the variance in profitability was directly calculated.

Behavioral titration experiment

A behavioral titration experiment was used to test predictions of the profitability model from July through November 1989. A behavioral titration is a set of dichotomous tests designed to determine how large a difference in the pay-offs or trade-offs between two options is required to elicit a change in behavior. Our experiment examined whether differences in profitability between snails and crabs could induce kites to include crabs in their diet.

Eighteen free-ranging adult snail kites were simultaneously offered ten snails and ten crabs in the feeding trays. Sizes of snails and crabs were selected to serve as a behavioral titration to determine the roles of profitability in diet choice by offering three tests: (1) profitability of crabs = snails, (2) profitability of crabs > snails, and (3) profitability of crabs >> snails. Test 1 used medium-sized snails (43–52 mm) and crabs (37.0–38.9 mm) of equal profitability (0.193–0.268 kJ/s), test 2 used the largest crabs (39.0–45.0 mm) and medium-sized snails so that the profitability of crabs (0.269–0.664 kJ/s) > snails, and test 3 used the largest crabs and small snails (30–40 mm) so that the profitability of crabs >> snails (0.201–0.218 kJ/s).

After two 3-h trials to allow the birds to habituate to feeding from the trays, each individual was run through a series of three tests over 2 days, and given a simultaneous choice of snails and crabs of different sizes. A 3-h test was long enough to permit kites to feed until satiation, since kites typically eat only 10–15 snails a day (Beissinger 1987). Tests were considered complete when at least three food items (the minimum number to demonstrate a preference) and no more than eight (ten is the absolute allowable maximum but 1–2 prey items might be less visible or in the corners of the feeding trays) were chosen within a 3-h period. The order in which tests were conducted was randomized. No more than one experiment per kite was conducted per morning (0630–1300 hours) or afternoon (1400–1900 hours) period. The identity of a chosen food item, order chosen, and handling time were noted. Between consecutive tests, trays were emptied and left in place.

We developed diet choice predictions for the behavioral titration experiment following the approach of Schoener (1969a, b) and Stephens et al. (1986). Our experiment is similar to the example of a hawk choosing among two prey types in a flock used by Stephens et al. (1986) to develop their model for prey encountered both simultaneously and sequentially. When sitting on an experimental perch, a kite looked down and viewed both trays simultaneously as one patch with 20 food items of two types. Within a prey type, each animal was approximately the same size and of equal profitability. Thus, kites had to make a choice between prey types rather than among prey items of a given type. In each foraging bout, a kite could choose either one snail or one crab, and the choice of a prey item was a mutually exclusive outcome. The long term average rate of energy intake (R) during tests of the behavioral titration experiment was calculated (Stephens et al. 1986) for different proportions of the diet composed of crabs (r):

$$R = \frac{re_c + (1-r)e_s}{\lambda^{-1} + rh_c + (1-r)h_s}$$

where λ is the encounter rate of food items, e is the energy and h is the handling time for snails (s) or crabs (c). This approach determines the energy and involvement time consequences (R) of various tactics (r) for exploiting the clump of 20 food items. Since each kite had the opportunity to encounter prey again after it finished eating by returning to the experimental perch, the experimental apparatus acted to ensure that encountering prey in the next bout could be instantaneous (λ=1). Ideally this experiment might have been designed to offer kites a choice of only one crab and one snail at a time, instead of multiple snails and crabs. However, it was usually impossible to refill experimental trays with prey after a capture without ending the experiment by scaring away the kite.

Novel food experiment

To test the effect of novel food items on food choice by kites, a large congeneric snail *(Pomacea urceus)* was offered in trays to 12 adult kites at the conclusion of their field trial in 1989. Kites have not been observed to eat *P. urceus,* which is found in deeper water than *P. doliodes* (Burky 1975; Burky and Burky 1977), although twice we found empty *P. urceus* shells under feeding perches. Because *P. urceus* is known to be eaten by other snail-eating birds such as limpkins *(Aramus guarauna)* (Beissinger, personal observation), it is unlikely to be noxious or distasteful to kites. Neither are there any striking physical characteristics of *P. urceus,* other than size, that differ from *P. doliodes,* which might discourage kites from eating them. The shell of *P. urceus* is a slightly darker brown and has many raised ridges compared to *P. doliodes,* which has a smooth and lighter brown shell.

Kites were offered five-ten medium to large sized *P. urceus* ranging in shell length from 50–110 mm, as large as or larger than *P. doliodes* but within the size and weight range of crabs. Data collected were identical to those collected during the behavioral titration experiment.

Table 1 The amount of time (s) required by 14 snail kites to open and eat *Pomacea doliodes* snails during field trials, broken into the three components of handling time. Correlations with snail size (r) were performed on natural log transformed data

Components of handling snails	N	Mean +SD	Median	Range	r
Remove operculum	138	28±24	21	6-208	0.110
Extract body	132	25±10	24	3-61	0.093
Eat body	160	40±25	35	1-168	0.659*
Total handling time	169	90±39	80	22-249	0.469*

* P<0.001

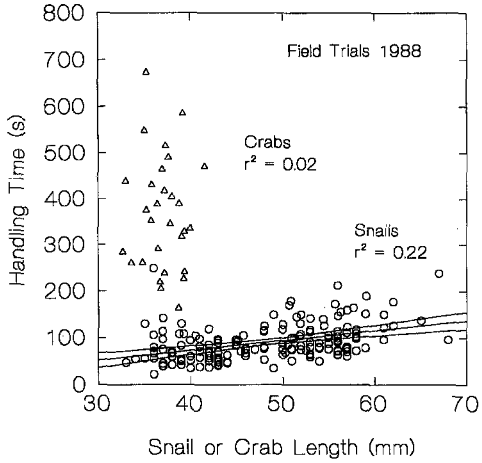

Fig. 1 The relationship between the amount of time required to open and eat a food item (handling time) by snail kites, and the size of *Pomacea doliodes* snails *(circles)* and *Dilocarcinus dentatus* crabs *(triangles)* during field trials. The regression line and 95% confidence interval are shown for snails. No significant correlation was found for crabs. See text for results of the statistical tests. Although the range of crab lengths was smaller than snail lengths, crabs were actually larger than most snails because they were wider

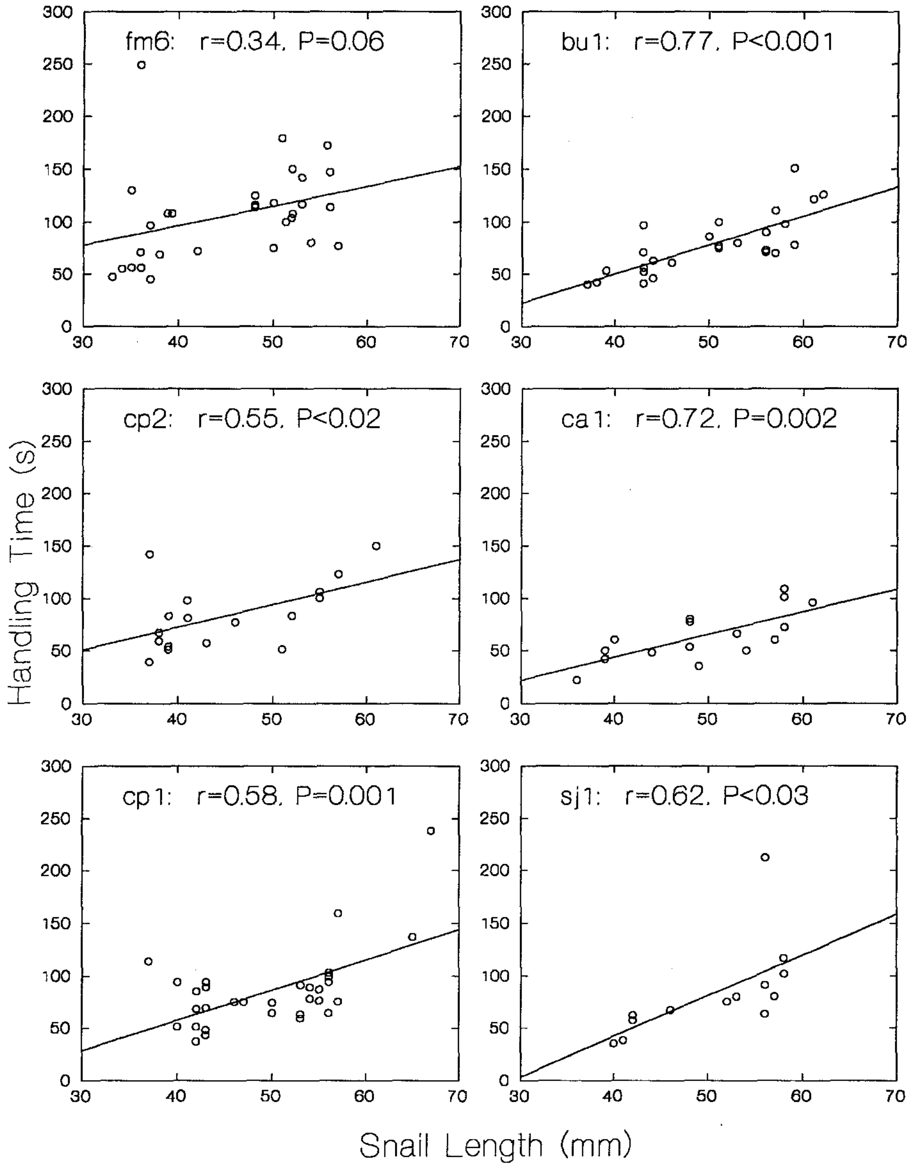

Fig. 2 The relationship between the size of *Pomacea doliodes* snails and handling time for six snail kites that were observed repeatedly during field trials. A Pearson correlation coefficient, its significance value, and a regression line are given for each bird

Results

Field trials

Handling times of *P. doliodes* snails by kites averaged 90 s (Table 1). The most time consuming component of handling a snail was the amount of time required to eat the body once it was removed from the shell. This often required tearing the body into several pieces and swallowing them one at a time, and on average comprised 44% of the total handling time. Eating the snail's body required significantly more time than removing the operculum or extracting the body from the shell ($F_{2,427}$ = 19.2, $P<0.001$); the latter two components of handling time did not differ from each other (Tukey hsd, P = 0.75).

The amount of time to open, extract and consume a snail was positively related to snail size (Fig. 1). Snail size alone accounted for 22% of the variation in handling time. The relationship between handling time and snail size was primarily a result of the strong correlation between snail size and the amount of time required to consume the body (Table 1); the other two components of handling time were not correlated with snail size (Table 1). Handling time was positively and consistently correlated with snail size (Fig. 2) for six individuals observed repeatedly ($n \geq 13$, $0.34<r<0.77$, $P<0.06$; ANCOVA for slopes: F=0.5, P=0.75), although differences in efficiency of processing snails existed among individual birds (ANCOVA for intercepts: F=7.8, $P<0.001$).

Few crabs were selected by kites during field trials (n=42) and they took nearly 4 times as long to eat as snails ($\bar{x}$=353 s). This difference was significant (t=23.5, $P<0.001$). Handling times for crabs had a larger range (162–706 s) and exhibited greater variation (SD=130 s) than for snails (Table 1). Furthermore, the amount of time required by kites to eat crabs was not related to crab size (r^2=0.02, n=30, P=0.43) (Fig. 1).

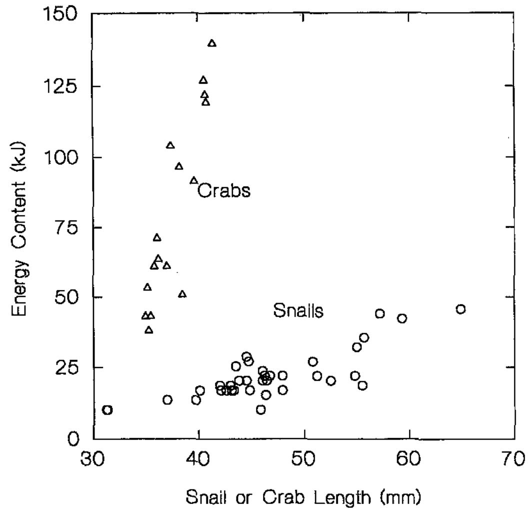

Fig. 3 The relationship between snail *(circles)* or crab *(triangles)* size and the total energy content of the animal based on the dry weight and energy content of parts ingested by snail kites. The natural log of energy content was strongly related ($P<0.001$) to snail length ($r^2=0.65$) and to the natural log of crab length ($r^2=0.77$). See the methods section for criteria for choosing different functions for snails and crabs

Modeling profit and risk for snails and crabs

Crab tissue had a higher energy value (25.37 kJ/g) than snail tissue (16.91 kJ/g). Crabs were also heavier and had greater dry weights of edible flesh than snails. Dry weights (d) were highly related ($P<0.001$) to body length for both snails (s) and crabs (c):

$$\ln d_s = 0.042 \times L_s - 1.765;\ (r^2 = 0.65, n = 36)$$
$$\ln d_c = 6.31 \times \ln L_c - 21.80;\ (r^2 = 0.77, n = 16).$$

Thus, the total energy of crabs was generally much greater than that of snails, and the total energy of both foods was highly related to body length (Fig. 3).

Relationships between food size and handling time were used for foraging costs. The best regression between handling time (t) and snail length ($r^2=0.22$, $n=166$) was:

$$t_s = 2.05 \times L_s - 10.74.$$

For crabs, an average handling time ($t_c=353$ s) was used because handling times were not significantly related to crab size.

Equations for profitability (P) were constructed using the expected values for energy content and handling time for food items as a function of size:

$$P_s = \frac{16.91 \times e^{(0.042\times L_s - 1.765)}}{(2.05 \times L_s - 10.74)}$$

which was simplified to

$$P_s = \frac{e^{(0.042\times L_s + 1.063)}}{(2.05 \times L_s - 10.74)}$$

and

$$\ln P_c = \ln 25.37 + (6.31 \times \ln L_c - 21.8) - \ln 353$$

which was simplified to

$$P_c = \frac{L_c^{6.31}}{e^{24.4329}}$$

Snails were more profitable than all but the largest crabs, which yielded the highest net energy returns (Fig. 4). Profitability rose slowly as snails got larger, primarily because energy returns only slightly outpaced handling costs as size increased. However, profitability of crabs increased rapidly with size because handling time did not depend on crab size, and small changes in crab size resulted in large changes in crab dry weight and total energy (Fig. 3).

Although large crabs were more profitable than snails, they were also likely to be more variable than snails in their reward rates to kites. Such variance depends on the perception of the forager (Real 1991) and may have two components for kites. First, variance in reward rate differs between food types. Variation in handling time is much greater for crabs than snails, so the variance in profitability should be greater for large crabs than for snails. Monte Carlo simulations found that variation in profitability of large crabs (SD=0.18 kJ/s) was greater than snails (SD=0.12 kJ/s). This difference, when cumulated over the handling time for a food item, becomes even more exaggerated because the time required for handling crabs is nearly 6 times more than for snails. Second, variance differs among food items of different sizes. Variation in reward is much larger among sizes of crabs than among snails due to the slopes of the profit-

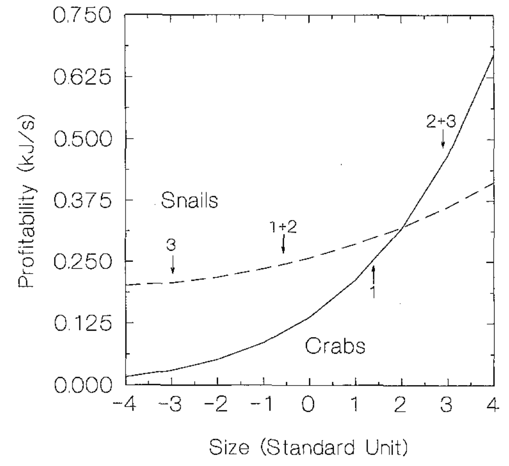

Fig. 4 Allometric relationships for profitability for *Pomacea doliodes* snails and *Dilocarcinus dentatus* crabs selected by free-flying snail kites. See text for the profitability equations. To compare profitability between snails and crabs of different sizes, the size of food items was standardized within food type by dividing the size range into nine equal intervals (snails: 30, 35, 40, ... 70; crabs: 25.0, 27.5, 30.0, ... 45.0) for graphical purposes. *Arrows* indicate the midpoint of snail and crab sizes offered to kites during the behavioral titration experiment, and *numbers* indicate the particular test

ability curves (Fig. 4). A misperception of size leads to greater differences in expected reward rates for crabs than for snails. This can be seen by comparing the rate of change of profitability among snails and crabs of different sizes (Fig. 4). Because kites specialize on snails, error in estimating true size is likely to be greater for crabs than for snails. Thus, reward rates for large crabs may always be more variable or risky than for snails.

Testing diet predictions with a behavioral titration experiment

A behavioral titration experiment was conducted to test if kites chose food on the basis of profitability by offering crabs that were equally, more, and much more profitable than snails (Fig. 4). Predictions of diet choice for this experiment can be made, based on the rate of energy gain from diets differing in the proportion of snails and crabs (Fig. 5). If snail kites try to maximize their short-term energy intake, they should choose the most profitable food item (Waddington and Holden 1979; Stephens et al. 1986). Thus, kites would maximize short-term energy intake by taking either snails or crabs in test 1, and switching to crabs in test 2 and especially in test 3 (Fig. 5). For long-term rate maximization, crabs should be chosen in all three tests (Fig. 5), because all crabs offered contained more energy than snails (Fig. 3) and were of equal or greater profitability (Fig. 4). A mixed diet of crabs and snails would be less profitable than a diet of only crabs, but would yield greater mean energy than eating only snails (Fig. 5). These predictions also follow general rules for maximizing the long-term rate of energy intake when encountering two prey types simultaneously (Stephens et al. 1986). However, kites might avoid choosing large crabs if eating crabs resulted in a large variance in reward rates (i.e. risk-averse foraging). Thus, if kites foraged in a risk-sensitive manner, they should choose snails over crabs in all three test.

Snail kites rarely chose crabs when also given the opportunity to feed on snails (Fig. 6). Of 289 food items chosen, only 45 (15.6%) were crabs. Half of 18 kites tested did not eat crabs, and only 3 birds chose more crabs than snails. When offered snails and crabs of equal profitability (test 1), 15 of 16 kites chose snails more frequently than crabs and the other individual chose equal numbers of the two foods (Fig. 6). When offered crabs that were more or much more profitable than snails, only 2 of 16 birds and 3 of 18 birds ate more crabs than snails

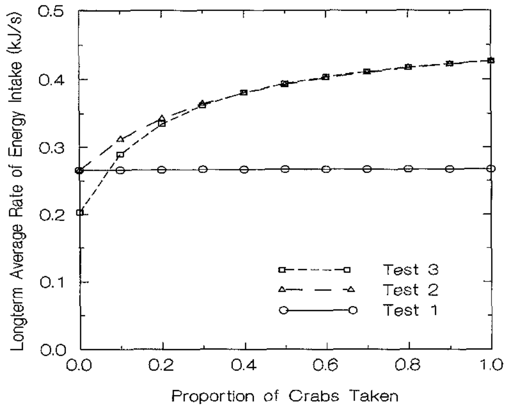

Fig. 5 The long-term average rate of energy intake (*R*) for potential diets composed of differing proportions of crabs and snails based on typical sizes of food offered to snail kites during the three tests of the behavioral titration experiment. See the methods section for calculation of *R*. Each test controlled the sizes of snails and crabs offered. Test 1 used medium-sized snails and crabs of approximately equal profitability (0.26 kJ/s), test 2 used the largest crabs and medium-sized snails so that the typical profitability of crabs (0.43 kJ/s) was greater than snails, and test 3 used the largest crabs and small snails so that the average profitability of crabs was much greater snails (0.20 kJ/s). See Fig. 4 for a graphical representation of the profitability of snails and crabs offered in the three tests

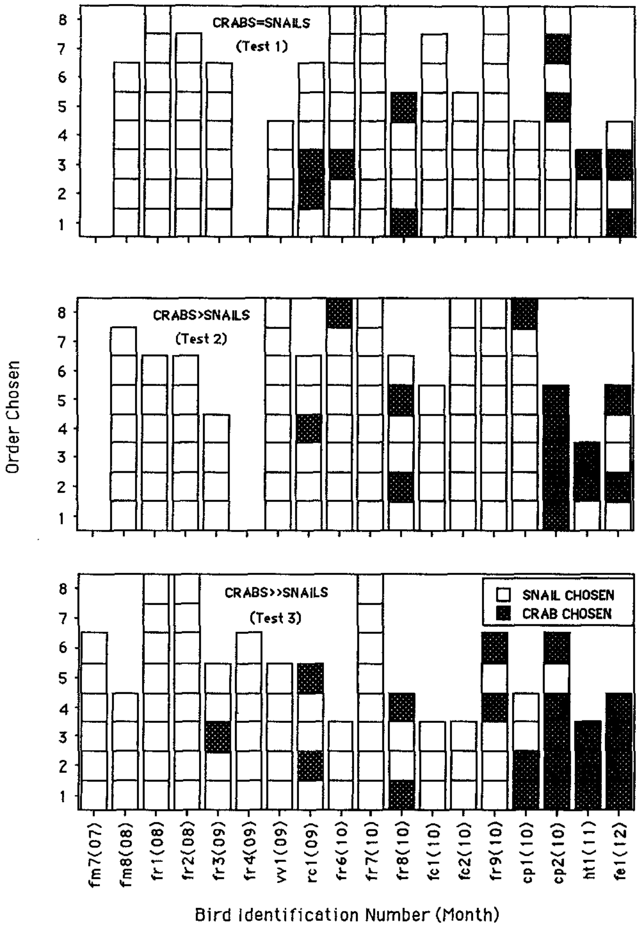

Fig. 6 Food items chosen by 18 free-flying adult snail kites during behavioral titration experiments to determine the role of profitability and risk in diet choice. The order that each food item was chosen is shown for snails *(open squares)* and crabs *(closed squares)*. Individual birds are arranged on the *x*-axis by chronological order of testing (month in parentheses). Test 1 used medium-sized snails and crabs of equal profitability, test 2 used the largest crabs and medium-sized snails so that the profitability of crabs>snails, and test 3 used the largest crabs and small snails so that the profitability of crabs>>snails

in tests 2 and 3, respectively. Kites that often chose crabs (Fig. 6) had not learned to handle them more efficiently (t=0.5, P=0.6) than kites that rarely ate crabs. Although the percentage of crabs chosen increased from 10.3% in test 1 to 13.9% ion test 2 and 23.1% in test 3 (χ^2=6.2, df=2, P<0.05), the increase was mostly due to the three individuals who switched from snails to crabs according to profitability rules (cp2, ht1, fe1; Fig. 6). Most other birds ate crabs at approximately the same frequency throughout the three tests. However, crabs were eaten more frequently during the latter part of the study than during earlier months (Fig. 6).

Handling times were measured during the choice experiments as a check to determine if model parameters and assumptions (Fig. 4) were upheld. As in field trials, handling times were positively related to snail length (r^2=0.47, n=105, P<0.001) and also for five individuals observed repeatedly (0.60<r<0.88, P≤0.01). However, the slope of the regression was higher (t_s=5.5×L_s−150.9), which would result in increased and decreased snail profitability estimates for small and large snails, respectively, and yield a flatter profitability function across snails of all sizes (Fig. 4). Unlike field trials, crab size was significantly related (r^2=0.31, n=37, P<0.01) to handling time during the experiments. If a regression of handling time on crab size for both years combined (t_c=17.3×L_c−220.1) was used instead of a mean handling time to estimate profitability (Fig. 4), crab profitability would be lower but it would still be equal or greater than snail profitability for the largest crabs. These analyses indicate that neither the basic predictions of the model nor the expected outcomes of the three tests would be changed.

During the course of the behavioral titration experiment, four young kites that had just fledged from the nest captured food from the feeding trays. Their choice of prey is interesting because it yields insight into the ontogeny of diet choice in kites. The fledlings chose 42 food items from our trays. Three of the four birds showed no preference for snails, choosing nearly equal or greater numbers of crabs, while one fledging fed only on snails.

Novel food experiment

Five of the 12 kites chose not to capture *P. urceus* snails. The other 7 birds captured 14 snails of which we were able to observe the fate of 12 snails. Eight of the 12 snails that were chosen were dropped immediately (<10 s) after capture, without attempting to extract the snail from its shell. Once snails were dropped, the birds made no effort to retrieve them. *P. doliodes* was rarely dropped after capture, and when this did occur, kites usually descended to the water's surface to retrieve the snail. The four novel food items that were eaten were handled as efficiently as *P. doliodes* ($\bar{x}$=133±89 s) when compared to crabs. During these tests, kites sometimes exhibited behaviors typical of neophobia (Coppinger 1969, 1970): escape behavior (flying away), alarm calls (vocalizations), and displacement behavior (preening). Thus, despite being offered a new food similar in appearance, behavior, and handling time to their preferred food, few kites chose to consume it.

Discussion

Snail kites may be preadapted to feed on crabs and frequently ate them during months when crabs attained their largest sizes (Beissinger 1990a; Donnay and Beissinger 1993). Since large crabs were more profitable than snails (Fig. 4), the inclusion of crabs in the diet might have occurred because kites switched to the more profitable food (Figs. 4, 5). But when given the choice, most kites preferred sizes of snails that were much less profitable than crabs (Fig. 6), avoided food with more variable reward rates (crabs), and rejected novel food items.

These results do not exclude other factors that could affect diet choice in this situation, but we believe such factors are unlikely to explain why snail kites ate or avoided eating crabs. Although crabs were eaten more frequently during the last months (October – December) than during the first months (July – September) (Fig. 6), sudden seasonal changes in diet needs seem unlikely since kites survive and reproduce well in Florida on diets composed completely of snails (Beissinger and Snyder 1987). A search image (Tinbergen 1960) should have been formed before three-quarters of the birds were tested, because crabs had already grown to large sizes by September (Donnay and Beissinger 1993) and were presumably encountered while hunting (Beissinger 1990a). It seems unlikely that kites would choose food to minimize time (Schoener 1969a, 1971) because nonbreeding birds can exceed their energy needs by spending less than 20% of their daylight hours foraging (Beissinger 1983), and nesting birds spend less than half of their day foraging (Beissinger and Snyder 1987; Beissinger 1987). To minimize time, kites should have chosen large crabs since eating crabs offered 3–6 times more energy (Fig. 3) and 3–5 large crabs would fullfill a kite's daily energy needs (400–700 kJ/day; Beissinger 1987) in 10–90% less time than eating snails (10–16 large or 30–50 small snails). Snail kites might have avoided eating crabs if they lacked the ability to digest them (Martinez del Rio and Stevens 1988), although such adaptations are not known for flesh-eating birds of prey. Moreover, adults from several populations have eaten crabs, turtles and small mammals, and have been kept in captivity on commercial zoo diets (Mader 1981; Beissinger et al. 1988, 1990b; Alves de Magalhães 1990). Also, some crabs were fed to nestlings or eaten by adults at 66% of the 80 nests that we observed in Venezuela (unpublished data). Finally, crabs did not appear dangerous to eat (Forbes 1989) because adult kites in our tests were never injured and had no difficulty avoiding the claws, although juveniles occasionally dropped crabs while handling them.

Snail kites were reluctant to switch from their specialized food to a prey that was more profitable when both foods were offered in abundant quantities. Profitability for large crabs was estimated to be 15–75% greater than profitability for large snails and 1–3 times greater than for small snails (Fig. 4), so it seems likely that the food items offered to kites were above a point that should have elicited a switch. Such a switch was noted for only 3 of 18 individuals (Fig. 6). Even when the profitability model was parameterized using values obtained during the behavioral titration experiments, profitability estimates for large crabs remained equal to or greater than those for large snails. We conclude that kites apparently did not choose among prey types based only on profitability rules, although kites tended to select the largest snails first from the feeding trays (Bourne 1985a; Beissinger, unpublished data). Bourne (1985b) likewise suggested that kites might not use profitability as a cue in patch choice decisions. However, he calculated profitability assuming that handling time was unrelated to snail size (also see Beissinger 1983), which was clearly refuted in this study (Figs. 1, 2).

Inherent variation in reward rates and diet choice

The avoidance by kites of a food that was more profitable, yet more variable in its reward to the forager, suggests that risk-averse behavior could serve to maintain specialization on snails. Few studies have demonstrated the avoidance of variable reward rates with a predator in its natural environment (Cartar 1991), although risk-averse behavior in the laboratory has been shown to affect foraging decisions of diet generalists under varying conditions of food availability (Caraco 1981; Real and Caraco 1986; Wunderle and Cotto-Navarro 1988; Tuttle et al. 1990). In those situations, risk of reward was equated with variance in food (gross energy) intake rates influenced by variable encounter rates, and foragers were most affected by risk under conditions of starvation. However, it is often difficult to ascertain how animals view risk because of our superficial understanding of animal cognition. We have invoked risk in a different manner but similar to that of Sutherland and Anderson (1987) and Cartar (1991). "Risk of reward" for foraging kites could have resulted from inherent variation in net intake rates due to differences in (1) the variability in efficiency of processing food (handling time) between snails and crabs (Fig. 2), and (2) the rates of change of profitability among snails and crabs of different sizes (Figs. 3, 4).

Variation in handling time was consistently greater for crabs than for snails. Furthermore, uncertainty in reward was magnified for crabs because handling time was poorly related to size and hence was much less predictable than handling time for snails, which increased with size (Figs. 1, 2). The relationship between handling time and snail size was primarily a function of the time required to eat the body and not the time needed to open the snail or extract the meat (Table 1). This result should not be surprising. The specialized trophic morphology of the kite should permit it to be equally skilled at preparing (e.g. removing the operculum and detaching the body from the shell) most sizes of snails to be eaten, whereas the time required to tear pieces of meat and swallow them should increase with snail size irrespective of any trophic specialization. Handling time can influence diet choice decisions (Keating et al. 1992) and variation in handling time should be an additional universal risk for foragers (Sutherland and Anderson 1987). However, variance in handling time may often be relatively predictable, and is probably easy for predators to assess compared to variation in encounter rate.

Variation in the rates of change of profitability was higher among crabs than snails of different sizes (Fig. 4), and results in uncertainty in reward if prey size is easily misconstrued. Snail kites may have difficulty determining the true size of snails and crabs because they must assess prey size by looking down through the water surface. The inability to discriminate between prey types when foraging at 3–6 m above the water has been suggested to cause kites to mistake *Marisa* snails for *Pomacea* snails (Snyder and Kale 1983). Looking from air into water causes size distortion and presents problems for other aquatic foragers (Labinger et al. 1991; Lotem et al. 1991). The consequences of such errors are much greater for crabs than for snails because the rate of energy gain for crabs is much more strongly affected by changes in size (Fig. 3). Risk from mistakes in assessing prey may be important only in situations where assessing prey size is difficult and when the profitability ranking of prey can become transposed due to changes in profitability with prey size (Fig. 4).

Neophobia and diet choice

In addition to minimizing risk of reward, snail kites may have avoided crabs simply because many kites were not willing to sample new or different foods. Tests with a novel food item showed that very few kites would eat it, even though the novel food *(P. urceus)* was very similar in general appearance and phylogenetic characteristics to their preferred food. Sometimes during these tests kites exhibited behaviors typical of neophobia (Coppinger 1969, 1970; Greenberg 1983). Nevertheless, kites may not always have distinguished that the food item was novel until after capturing it, when they should have been able to feel the raised ridges of the *P. urceus* shells and their extra weight. Kites usually responded to these cues by dropping the unfamiliar snails without even trying to open them. Avoidance of food based on novelty is difficult to demonstrate because it depends on the absence of selection. A more conclusive test for neophobic responses would have been to offer kites a wider variety of food types and compare their responses to a predator with a broader diet (e.g. Greenberg 1987). But it is unlikely that kites would have eaten most other food items, given the rarity of other foods in their diet (Beissinger et al. 1988, 1990a) and the difficulty in getting most free-flying kites to select a congeneric snail, or a crab they were known to eat.

Avoidance of new food items may be a response that is learned by snail kites. Kites newly fledged from the nest did not display a preference for *P. doliodes* snails but instead frequently took crabs from the feeding trays, whereas half of the adults tested never sampled crabs. To understand diet choice decisions by this specialist, it may be important to understand more about the ontogeny of diet selection. Trial-and-error frequently plays an important role in the development of food recognition and diet selection in young birds (Edwards 1989; Wunderle 1991). Typically, juveniles are less proficient than adults at the foraging maneuvers which require the most skill or time to master, and often for raptors this involves prey recognition and capture (Wunderle 1991). Fledgling kites quickly learn to catch snails as efficiently as adults, but do not become as proficient as adults at handling snails until 3 months after fledging (S. R. Beissinger, personal observations). We have no comparable data on the ontogeny of kite handling times for crabs. However, if juvenile kites respond to variance in handling time when sampling different food items, or if the handling time of juveniles improves for snails but not for crabs, then handling time could play a role in the ontogeny diet specialization in snail kites.

Behavioral conservatism, morphological costs, and diet specialization

Although morphological adaptations allow kites to specialize on snails, extreme specialization in this predator does not appear to be maintained solely by the costs of specialization (Levins 1968; Schoener 1971; MacArthur 1972). Costs of specialization imposed by morphology on the efficiency of food processing may occur (Benkman 1988; Meyer 1989), but such costs were overcome for kites when the profitability of alternative food increased sufficiently. Yet kites rarely chose large crabs over snails (Fig. 6). Thus, such trade-offs alone may not be required to maintain specialization. Instead, our study suggests that behavioral conservatism may also play a role in maintaining diet specialization in the snail kite.

Behavioral conservatism is a syndrome of responses that individuals can display when they encounter risks, or face new or less familiar situations. Individual- and species-specific differences in risk-taking or responses towards novel stimuli are indicative of different degrees of willingness to incur variation. For a forager, the perception of risk derives not only from the variance in reward rates but also from a variety of cognitive processes including the forager's proficiency in estimating relevant prey qualities, its recent experience with alternate prey items, and its evolutionary "memory" of those items that are most likely to result in the highest rewards (Real 1991). These cognitive processes are nested within an individual's or species' psychological predisposition toward novelty. Such a predisposition will depend upon the degree that an organism is sensitive to, aware of, and exhibits a preference for, a limited range of a larger complex stimuli (Klopfer 1967; Greenberg 1983). Species that choose a smaller range or avoid risk are behaviorally conservative. Although behavioral conservatism acts as a proximate factor in diet choice, it is also an evolutionary process under the direction of natural selection because it can increase efficiency or survival by limiting exposure to new food items, which are likely to be less profitable, or new situations, which are likely to be risky.

For snail kites, both minimization of risk-of-reward and avoidance of new food items appear to play a role in maintaining extreme diet specialization. That kites rarely chose crabs in our experiments when snails were available is in accord with field observations that alternative foods are eaten by kites primarily when snails are unavailable (Beissinger 1990a). Under conditions of food shortages, even the most risk-averse forager will choose a risky item if the reward is high enough (Real and Caraco 1986; Cartar 1991). Differences between individuals in the perception of when a reward is "high enough" might have caused some kites to switch to crabs before others. The inclusion of crabs in the diet of kites occurred during months when crabs had grown to full size and the ratio of small to large crabs was at its lowest (Donnay and Beissinger 1993). Also during these months the foraging areas of kites become choked with vegetation, which hinders the capture of snails (Beissinger 1983). Thus, kites seemed more willing to incur the risks of eating crabs under conditions of lower snail encounter rates and when the chance of capturing a large, profitable crab was the greatest. During other times, kites may simply prefer snails because they are more profitable (Fig. 4) and more abundant than crabs (Donnay and Beissinger 1993). Nevertheless, some individuals in our experiment might have switched to crabs because they were able to eat them efficiently. But kites that often chose crabs did not require less time to handle them than birds that rarely ate crabs. Calculating profitabilities of snails and crabs for individual kites might help to refine diet choice predictions, but our data were not sufficient to address this.

Behavioral conservatism may have important implications for the evolution of specialization in vertebrate predators. It is easy to imagine how specialization in certain foraging techniques or behaviors by individuals within a population (e.g. Price 1987; Werner and Sherry 1987) could develop and be maintained by the establishment of conservative behavioral repertoires that limit the variance in reward rates or exposure to new (most likely less profitable) food items. If diet specialization is maintained in vertebrate predators by behavioral conservatism, then specialization may be reversible (Futuyma and Moreno 1988) only if the behaviors that reinforce specialization are eroded.

Unfortunately, a role for behavioral conservatism in diet specialization only adds to the confusion of whether morphological evolution is driven by behavior, or whether behavioral specialization is a result of morphological specialization, or both (Sutherland 1987; Krebs 1991). Given the close links sometimes observed between variation in trophic morphology and foraging behaviors (e.g. Price 1987), it is possible that selection on one trait could drag along the other. For example, selection for behavioral conservatism should be strong in species that are least likely to be able to handle or digest new food efficiently, such as those with morphological specializations, and more relaxed in species that are better equipped morphologically or physiologically to process a greater variety of food items relatively efficiently. It may, however, be difficult to untangle if one process came first, and past studies have incompletely approached the problem.

For example, the maintenance of severe diet specialization by behavioral conservatism in snail kites appears to be the antithesis of the historical conditions of morphological novelty that are thought to promote the evolution of specialization in crossbills (Benkman and Lindholm 1991). Do these results reflect differences in evolutionary scenarios, or were they simply due to different emphases and methodological approaches? We evaluated the profitability of alternative foods, offered both alternative and novel foods to adult and juvenile kites, and then noted their diet selection, whereas Benkman and Lindholm (1991) altered the bills of crossbills for comparison to a generalist seedeater to uncover the costs of different morphologies on feeding efficiency. Crossbills were more efficient than generalist feeders and small changes in bill size were related to food processing efficiency, but crossbills were not offered a simultaneous choice between preferred and alternative foods to compare profitabilities and test for behavioral constrains. In kites, conservative behavior constrained diet choice because alternative foods were actually more profitable than preferred foods, but the feeding efficiency of kites was not compared with the efficiency of a generalist raptor predator.

These two approaches – tests for behavioral conservatism and interspecific comparisons of morphological costs – should be incorporated in future research designed to understand the causes and consequences of ecological specialization. In some cases, either morphological costs or behavioral conservatism may clearly emerge as factors maintaining specialization. Results that support both would uphold the notion that both traits have roles in the maintenance of ecological specialization. When neither morphological costs nor behavioral conservatism can be demonstrated, other causes of specialization such as interspecific competition or resource availability constraints should be examined.

Acknowledgements We thank Tomas Blohm for the opportunity to live and work on his ranch, and other Venezuelan ranchers who provided access to their land. Funding was provided by the Smithsonian Institution's International Environmental Sciences Program in Venezuela. Pam Limberger, Franklin Suarez, Adriana Tami, and the Cabrere family assisted with field work. George Furnival helped with variance calculations. Craig Benkman, Tom Caraco, Russ Greenberg, Tom Schoener, Dave Stephens, Noel Snyder, Joe Wunderle, and two anonymous reviewers graciously improved various drafts of this paper. Beissinger thanks the International Institute of Tropical Forestry (USDA Forest Service) and the Department of Biology at the University of Puerto Rico for hospitality during the completion of this manuscript while he was a Visiting Scientist.

References

Alves de Magalhães C (1990) Hábitos alimentares e estratégia de forrageamento de *Rostrhamus sociabilis* no Pantanal de Mato Grosso, Brasil. Ararajuba 1:95–98

Beissinger SR (1983) Hunting behavior, prey selection, and energetics of snail kites in Guyana: consumer choice by a specialist. Am Nat 136:20–38

Beissinger SR (1987) Anisogamy overcome: female strategies in snail kites. Am Nat 129:486–500

Beissinger SR (1988) The snail kite of North American birds, volume IV. In: Palmer RS (ed) Handbook. Yale University Press, New Haven, pp 148–165

Beissinger SR (1990a) Alternative foods of a diet specialist, the snail kite. Auk 107:327–333

Beissinger SR (1990b) Experimental brood manipulations and the monoparental threshold in snail kites. Am Nat 136:20–38

Beissinger SR, Snyder NFR (1987) Mate desertion in the snail kite. Anim Behav 35:477–487

Beissinger SR, Thomas BT, Strahl SD (1988) Vocalizations, food habits, and nesting biology of the slender-billed kite with comparisons to the snail kite. Wilson Bull 100:604–616

Benkman CW (1988) Seed-handling ability, bill structure, and the cost of specialization for cross-bills. Auk 105:715–719

Benkman CW, Lindholm AK (1991) The advantages and evolution of a morphological novelty. Nature 349:519–520

Bourne GR (1985a) Field tests of micropatch and prey-size selection by snail kites *Rostrhamus sociabilis*. Ibis 127:141–147

Bourne GR (1985b) The role of profitability in snail kite foraging. J Anim Ecol 54:697–709

Burky AJ (1975) Growth and biomass production of an amphibian snail, *Pomacea urceus* (Müller) from the Venezuelan savannah. Proc Malacalog Soc Lond 41:127–143

Burky KA, Burky AJ (1977) Buoyancy changes as related to respiratory behavior in an amphibious snail, *Pomacea urceus* (Müeller), from Venezuela. Nautillus 91:97–104

Caraco T (1981) Energy budgets, risk, and foraging in dark-eyed juncos *(Junco hyemalis)*. Behav Ecol Sociobiol 8:213–217

Caraco T, Martindale S, Whittam TS (1980) An empirical demonstration of risk-sensitive foraging preferences. Anim Behav 28:820–830

Cartar RV (1991) A test of risk-sensitive foraging in wild bumble bees. Ecology 72:888–895

Coppinger RP (1969) The effect of experience and novelty on avian feeding behavior with reference to the evaluation of warning coloration on butterflies. I. Reactions of wild-caught adult blue jays to novel insects. Behaviour 35:45–60

Coppinger RP (1970) The effect of experience and novelty on avian feeding with reference to the warning coloration of butterflies. II. Reactions of naive birds to novel insects. Am Nat 104:323–337

Donnay TJ, Beissinger SR (1993) Apple snail *(Pomacea doliodes)* and freshwater crab *(Dilocarcinus dentatus)* population fluctuations in the llanos of Venezuela. Biotropica 25:206–214

Edwards TC Jr (1989) The ontogeny of diet selection in fledging ospreys. Ecology 70:881–896

Eisenberg JF (ed) (1979) Vertebrate ecology in the northern neotropics. Smithsonian Institution Press, Washington, DC

Ezekiel M, Fox KA (1963) Methods of correlation and regression analysis. Wiley New York

Forbes LS (1989) Prey defenses and predator handling behaviour: the dangerous prey hypothesis. Oikos 55:155–158

Futuyma DJ, Moreno G (1988) The evolution of ecological specialization. Annu Rev Ecol Syst 19:207–233

Greenberg R (1983) The role of neophobia in determining the degree of foraging specialization in some migrant warblers. Am Nat 122:444–453

Greenberg R (1985) The role of neophobia in foraging site selection of a tropical migrant bird: an experimental study. Proc Natl Acad Sci USA 81:3778–3780

Greenberg R (1987) Development of dead leaf foraging in a tropical migrant warbler. Ecology 68:130–141

Guilford T, Dawkins MS (1987) Search images not proven; a reappraisal of recent evidence. Anim Behav 35:1838–1845

Haverschmidt F (1962) Notes on the feeding habits and food of some hawks of Surinam. Condor 64:154–158

Haverschmidt F (1970) Notes on the snail kite in Surinam. Auk 87:580–584

Howell AH (1932) Florida bird life. Coward-McCann, New York

Keating JR, Robel RJ, Adams AW, Behnke KC, Kemp KE (1992) Role of handling time in selection of extruded food morsels by two granivorous bird species. Auk 109:863–868

Klopfer PH (1967) Behavioral aspects of habitat selection: a preliminary report on stereotypy in foliage preferences of birds. Wilson Bull 77:376–381

Krebs JR (1980) Optimal foraging, predation risk and territory defence. Ardea 68:83–90

Krebs JR (1991) The case of the curious bill. Nature 349:465

Labinger Z, Katir G, Benjamin Y (1991) Prey size choice by captive pied kingfishers, *Ceryle rudis* L. Anim Behav 42:969–975

Levins R (1968) Evolution in changing environments. Princeton University Press, Princeton, NJ

Lotem A, Schechtman E, Katir G (1991) Capture of submerged prey by little egrets, *Egretta garzetta garzetta:* strike depth, strike angle, and the problem of light refraction. Anim Behav 42:341–346

MacArthur RH (1972) Geographical ecology. Harper and Row, New York

Mader WJ (1981) Notes on nesting raptors in the llanos of Venezuela. Condor 83:48–51

Martin AC, Zim HS, Nelson AL (1951) American wildlife and plants: a guide to wild food habits. Dover, New York

Martinez del Rio C, Stevens BR (1988) Physiological constraint on feeding behavior: intestinal membrane disaccharidases of the starling. Science 243:794–796

Meyer A (1989) Cost of morphological specialization: feeding performance of the two morphs in trophically polymorphic cichlid fish, *Ciclasoma citrinellum.* Oecologia 80:431–436

O'Connell M (1989) Population dynamics of Neotropical small mammals in seasonal habitats. J Mammal 70:532–548

Partridge L, Green P (1987) An advantage for specialist feeding in jackdaws, *Corvus monedula.* Anim Behav 35:982–990

Price T (1987) Diet variation in a population of Darwin's finches. Ecology 68:1015–1028

Pyke GH (1984) Optimal foraging theory: a critical review. Annu Rev Ecol Syst 15: 523–575

Pyke GH, Pulliam HR, Charnov EL (1977) Optimal foraging: a selective review of theory and tests. Q Rev Biol 52:137–154

Real L (1991) Animal choice behavior and the evolution of cognitive architecture. Science 253:980–986

Real L, Caraco T (1986) Risk and foraging in stochastic environments. Annu Rev Ecol Syst 17:371–390

Richards LJ (1983) Hunger and the optimal diet. Am Nat 122:326–334

Schoener TW (1969a) Optimal size and specialization in constant and fluctuating environments: an energy-time approach. In: Diversity and stability in ecological systems (Brookhaven Symposia in Biology no. 22):103–114

Schoener TW (1969b) Models of optimal size for solitary predators. Am Nat 103:277–313

Schoener TW (1971) Theory of feeding strategies. Annu Rev Ecol Syst 2:369–404

Schoener TW (1979) Generality of the size-distance relation in models of optimal feeding. Am Nat 114:902–914

Sih A (1980) Optimal behavior: can foragers balance two conflicting demands? Science 210:1041–1043

Snyder NFR, Kale HW II (1983) Mollusk predation by snail kites in Colombia. Auk 100:93–97

Snyder NFR, Snyder HA (1969) A comparative study of mollusc predation by limpkins, Everglade kites, and boat-tailed grackles. Living Bird 8:177–223

Snyder NFR, Snyder HA (1970) Feeding territories in the Everglade kite. Condor 72:492–493

Stephens DW, Krebs JR (1986) Foraging theory. Princeton University Press, Princeton, NJ

Stephens DW, Lynch JF, Sorenson AE, Gordon C (1986) Preference and profitability: theory and experiment. Am Nat 127:533–553

Strong DR, Lawton JH, Southwood R (1984) Insects on plants: community patterns and mechanisms. Harvard University Press, Cambridge, Mass

Sutherland WJ (1987) Why do animals specialize? Nature 325:483–484

Sutherland WJ, Anderson CW (1987) Six ways in which a foraging predator may encounter options with different variances. Biol J Linn Soc 30:99–114

Sykes PW Jr, Kale HW II (1974) Everglades Kites feed on non-snail prey. Auk 91:818–820

Tinbergen L (1960) The natural control of insects in pine woods. I. Factors influencing the intensity of predation by songbirds. Arch Neer Zool 13:265–343

Tuttle EM, Wulfson L, Caraco T (1990) Risk-aversion, relative abundance of resources and foraging preference. Behav Ecol Sociobiol 26:165–171

Voous KH, van Dijk T (1973) How do snail kites extract snails from their shells? Ardea 61:179–185

Waddington KD, Holden LR (1979) Optimal foraging: on flower selection by bees. Am Nat 114:179–196

Weller MW (1967) Notes on some marsh birds of Cape San Antonio, Argentina. Ibis 109:391–411

Werner TK, Sherry TW (1987) Behavioral feeding specialization in *Pinaroloxias inornata,* the "Darwin's finch" of Cocos Island, Costa Rica. Proc Natl Acad Sci USA 84:5506–5510

Wilkinson L (1990) SYSTAT: the system for statistics. Systat Inc., Evanston, Ill

Woodin MC, Woodin CD (1981) Everglade kite predation on a soft-shelled turtle. Fla Field Nat 9:64

Wunderle JM Jr (1991) Age-specific foraging proficiency in birds. Curr Ornithol 8:273–324

Wunderle JM Jr, Cotto-Navarro Z (1988) Constant versus variable risk-aversion in foraging bannaquits. Ecology 69:1434–1438