ANIMAL BEHAVIOUR, 2008, **75**, 2005–2011
doi:10.1016/j.anbehav.2007.11.009

The development and lateralization of prey delivery in a bill load-holding bird

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(Received 2 August 2007; initial acceptance 6 September 2007; final acceptance 5 November 2007; published online 23 April 2008; MS. number: A10835)

Laterality or the preferential use of one or the other side of the body is associated with differential brain activity and increased specialization of brain function. Right or left biases are widespread among vertebrates and have been documented among some birds. Bill load holding or the delivery of whole prey in a bird's beak is common among terns (Charadriiformes) and many other birds. We recorded more than 2000 Caspian tern, *Hydroprogne caspia*, chick-feeding events for analysis of lateralization of prey within the bills of adult birds, size and shape of prey items delivered to chicks in relation to chick age, and the development of prey-handling skills among chicks. No initial lateralization of prey head position was found as adults flew into the colony, but head position of successful feeds was found to be significantly lateralized with a bias to the right side. Adults switched prey orientation significantly more often from left to right than from right to left without dropping the prey item, suggesting an adult bias. Adults appeared to adjust the length but not the shape of prey delivered according to chick age. Ability of chicks to manipulate prey items increased with age. Lateralization was most obvious in the first week of a tern's life, and adults modified their delivery behaviour to respond to these changes. Bill load-holding birds are excellent subjects to study lateralization of feeding behaviour in the wild and they may allow integration of lateralization with developmental changes.

Keywords: Caspian tern; chick rearing; *Hydroprogne caspia*; lateralization; prey delivery

Laterality is the different use of one or the other side of the body and is often reflective of hemispheric asymmetry and increased specialization of brain function (Güntürkün et al. 2000; Ventolini et al. 2005). Historically, lateralization has been considered a uniquely human trait associated with language and handedness (Bisazza et al. 1998). Within the past 30 years, however, motor and sensory directional lateralization (i.e. right or left side bias) at the population level is widespread among vertebrates, from bony fish, to amphibians, reptiles, birds and mammals (Rogers & Andrew 2002; Malashichev & Deckel 2006). In this study, we focus on three aspects of prey handling by a bill load-holding piscivorous bird during chick rearing: lateralization of prey head position within an adult's bill, the association between chick age and prey characteristics, and the development of prey manipulation skills among chicks. Piscivorous bill load holding is the behaviour of transporting whole fish in the beak for the purpose of courtship or chick rearing. We show that bill load-holding birds make excellent subjects for studying lateralization in the wild, especially when observations are focused on young chicks. Motor and sensory lateralization has been documented in at least 10 of the 29 avian orders, including Falconiformes (Palleroni & Hauser 2003), Strigiformes (Csermely 2004), Galliformes (Rogers 2002; Valenti et al. 2003), Charadriiformes (Ventolini et al. 2005), Columbiformes (Prior et al. 2004), Passeriformes (Franklin & Lima 2001; Templeton & Gonzalez 2004; Wiltschko et al. 2004), Gruiformes and Anseriformes (Randler 2005), Psittaciformes (Harris 1989) and Coraciiformes (Rogers 2002). Among these there is some evidence for homology in direction of lateralization, with the left hemisphere (right eye) associated with feeding decisions (Rogers et al. 2007) and categorization (McKenzie et al. 1998), and the right hemisphere (left eye) controlling spatial maps (Tommasi et al. 2000), novelty (McKenzie et al. 1998) and emotional reactions (e.g. aggression, fear;

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0003–3472/08/$34.00/0

Vallortigara et al. 2001). Despite these striking similarities in patterns of hemispheric control, there remain many exceptions (e.g. Franklin & Lima 2001), so it is valuable to question whether direction of lateralization is an arbitrary result of ecological and embryological factors (Rogers 1997) or reflects early homology in avian hemispheric dominance. In any case, the direction of lateralization is probably of secondary importance to the fact that different functional specialization of the two hemispheres of the brain exist (Vallortigara et al. 1999; Rogers et al. 2004).

Feeding and prey capture are lateralized in several avian species, including pebble/grain discrimination in the domestic chick and hen, *Gallus gallus*, quail chick, *Coturnix coturnix*, and pigeon (McKenzie et al. 1998; Güntürkün et al. 2000; Valenti et al. 2003; Rogers et al. 2007), eye-use during prey capture in the black-winged stilt, *Himantopus himantopus* (Ventolini et al. 2005), visual foraging in the zebra finch, *Taeniopygia guttata* (Alonso 1998), approach towards adults during begging in the Australian magpie chick, *Gymnorhina tibicen* (Hoffman et al. 2006), and tool manufacture and use in the New Caledonian crow, *Corvus moneduloides* (Rutledge & Hunt 2004; Weir et al. 2004). These last two behaviours, of the magpie and New Caledonian crow, are most similar to that of prey delivery in Caspian terns, *Hydroprogne caspia*, with which we are concerned. While tool use is certainly a very different behaviour from that of prey delivery, both involve an item that is held horizontally in the bill and manipulated into a hole, in terns, a fish into the mouth of chick. Two independent studies have shown that New Caledonian crows show individual laterality in tool use, with the working end of a stick oriented to the right or left of their beak (Rutledge & Hunt 2004; Weir et al. 2004), while tool manufacture is lateralized at the population level and corresponds to increasing difficulty of the manufacturing task (Hunt et al. 2001, 2006).

Terns of the order Charadriformes transport prey items, primarily whole fish, crosswise in their bills (heretofore called bill loads) during courtship and chick rearing (Collis et al. 2002). This conspicuous handling of meals makes terns ideal for studying the relationship between parental investment and prey characteristics because the prey are readily identified to type and prey size can be estimated (Cuthbert & Wires 1999). Because prey are held crosswise and asymmetrically, with the head to one side and the tail to the other side, bill load-holding birds are also suitable for investigating lateralization. As the world's largest tern, Caspian terns carry relatively large prey that are readily identified in the field (Larson & Craig 2006), and their colonial habits allow for large sample sizes in a relatively short time.

Caspian tern young are semiprecocial and seminidifugous, with typical clutches of one, two or three young per pair (Anderson 2003). Both parents begin delivering whole prey items to young at hatching (Quinn 1990). Typically, an adult lands near the nest scrape with a bill load and proceeds to walk towards its chick(s), which approaches, grabs the prey item from the adult's bill, and swallows it whole. If a chick is not aggressive in taking the item, the adult will lean down and make the item easier to obtain (Bent 1921). To our knowledge, ours is the first study to examine the orientation of prey in bills of adult Caspian terns, and we are aware of no other published work examining bill load-handling in birds.

Many studies have quantified prey delivery by bill load-holding seabirds during chick rearing. Prey size increases linearly with chick age in roseate terns, *Sterna dougallii* (Ramos et al. 1997), common terns, *Sterna hirundo* (Wiggins & Morris 1986) and black guillemots, *Cepphus grylle* (Cairns 1987), and with date in Caspian terns (Anderson et al. 2005). The availability of appropriate species and size of prey is critical to the reproductive success of common, *S. hirundo*, and Arctic terns, *S. paradisaea* (Uttley et al. 1989). The most detailed research of prey selection by Caspian terns has focused on the applied conservation problem of their depredation of endangered salmon species of the Columbia River, Oregon, U.S.A. (Roby et al. 2003; Ryan et al. 2003; U.S. Fish & Wildlife Service 2005). We believe that a thorough examination of a chick's introduction to prey is vital to understanding the natural and evolutionary history of bill load-holding birds, such as the Caspian tern, because both an adult's ability to deliver prey and a chick's adeptness at consuming prey are directly related to individual fitness.

METHODS

Our study was conducted primarily on East Sand Island, Oregon, U.S.A., in the Columbia River estuary at the largest Caspian tern colony in the world, with an estimated 8200 breeding pairs (Suryan et al. 2004). A secondary site was a breeding colony of an estimated 520 pairs at Brooks Island San Francisco Bay, California, U.S.A. Observations were conducted from blinds at both colonies. Data were collected in 2005 from mid-May, when chicks hatched, until the end of July, when most young had fledged.

Researchers opportunistically selected adult Caspian terns flying into the colony with fish (i.e. bill loads) and recorded the species and size of prey and the initial orientation of prey in the bill (right, left, lengthwise; see Fig. 1), the age and status (alpha, beta, pirate, adult) of birds attempting to acquire the prey, number and location (head, tail, middle) of each feeding attempt, and final prey orientation of successful feeding events, or outcome of the event if unsuccessful (kleptoparasitism, adult departed). A feeding attempt was defined as contact between a delivered prey item and a chick's bill, or a chick's visible lunging towards the delivered prey. Chicks that acquired the prey or that made the most contacts with or lunges towards the prey were considered 'primary chicks'. Only primary chicks were considered in this analysis. All feeding events were videotaped to aid in analysis of observations.

Prey orientation was defined as the head position of the prey item relative to the body of the adult carrying it (Fig. 1). Initial orientation was determined as soon as possible after the adult landed in the colony. Final orientation was defined as the last position of the prey item before ingestion or failure of the event.

Prey size was estimated in relation to adult bill length (Larson & Craig 2006). Prey species were visually identified based on a number of features and familiarity with the local

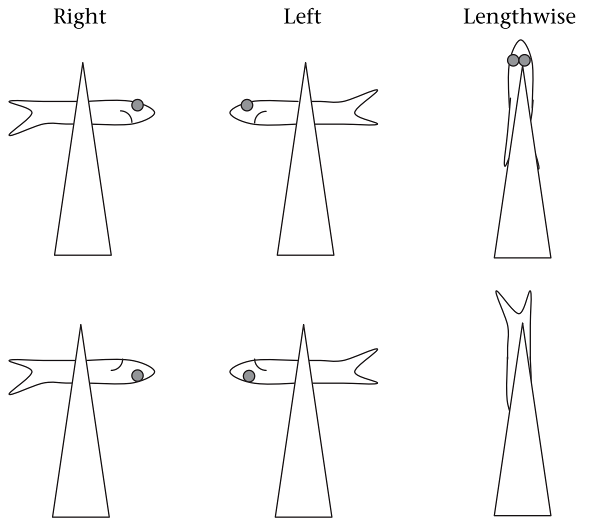

Figure 1. Possible orientation of prey items within the bills of adult Caspian terns.

species. Prey items were identified to the family level with the aid of spotting scopes and binoculars. If identification was impossible, the item was classified as unknown. Chick age was estimated to the nearest week based upon plumage and size differences (Fig. 2).

The families Engraulidae (anchovies) and Embiotocidae (perch) were used in fusiform and ovate comparisons. Although other fusiform species were observed, engraulids were the most distinctly fusiform of common prey items delivered. Embiotocids were the primary ovate prey items recorded in the colony.

RESULTS

Lateralization

Of 1344 successful chick feeds, 99.6% were swallowed head first. In lateralization analysis, only left and right orientations were considered because they comprised 99.6% of prey deliveries.

No initial bias for right or left orientation of the head of the prey item was found in adult Caspian terns as they landed in the colony (right head: $N = 680$; left head: $N = 677$; chi-square test: $\chi^2_1 = 0.007$, $P = 0.935$). Final prey orientation prior to successful chick feeds was significantly lateralized with a bias towards the right side (right head: $N = 633$; left head: $N = 541$; chi-square test: $\chi^2_1 = 7.21$, $P = 0.007$). When the prey type were analysed separately, the right bias for successfully ingested prey was significant for engraulids (right head: $N = 489$; left head: $N = 399$; chi-square test: $\chi^2_1 = 7.21$, $P = 0.002$), but not embiotocids (right head: $N = 144$; left head: $N = 140$; chi-square test: $\chi^2_1 = 7.21$, $P = 0.812$). Prey that were initially oriented to the left did not result in a greater number of feeding failures, drops or attempts by chicks than did prey that were initially oriented to the right. Prey orientation was switched significantly more often from left to right than from right to left before a successful feeding event (chi-square test: $\chi^2_1 = 28.55$, $P < 0.0001$).

When we examined lateralization based on chick age class, only deliveries to 1-week-old chicks showed significant lateralization of prey orientation, again with a right side bias (Table 1; chi-square test: $\chi^2_1 = 4.34$, $P = 0.037$), although there was a nonsignificant tendency towards the right side in all age classes. When 2-week-old chicks were grouped with all successive age classes, a significant bias towards the right was still found (chi-square test: $\chi^2_1 = 5.59$, $P = 0.018$).

Length and Shape of Prey

Mean length of prey delivered by adults and successfully swallowed by chicks increased linearly with chick age, reaching the maximum length when chicks were 3 weeks old (ANOVA: $F_{1,4} = 25.317$, $P < 0.001$; Fig. 3). These trends were also observed within a single day (14 June 2005), when prey availability was expected to be similar for all foraging adults (Fig. 4).

One-week-old chicks consumed only 60% of the ovate embiotocids delivered to them, significantly less than the 86% of fusiform engraulids delivered to them (chi-square test: $\chi^2_1 = 6.35$, $P = 0.0117$). After the first week there was no difference in the percentage of embiotocids and engraulids consumed by chicks, and the percentage of each prey type consumed continued to increase with chick age until reaching 100% at 5 weeks (Fig. 5). Adults ingested a higher proportion of embiotocids than did all other age groups. In this case, the adults either self-fed in the colony, or fed their mate/copulation partner.

Development of Prey-handling Skills

Caspian tern chicks that dropped a delivered prey item at least once had a higher rate of feeding failure than chicks that did not drop a delivered prey item (chi-square test: $\chi^2_1 = 389$, $P < 0.0001$). The rate of feeding failure correlated positively with the number of times that prey

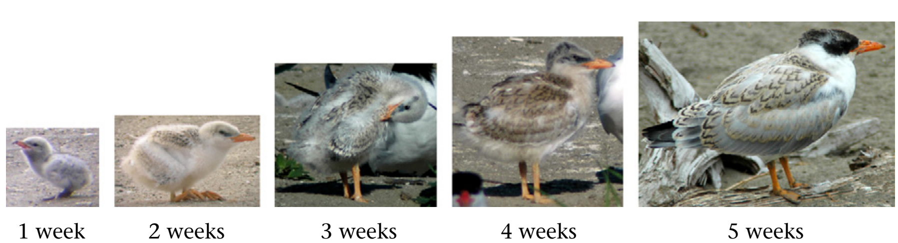

Figure 2. Average size and plumage of Caspian tern chicks in each age class (weeks 1−5).

Table 1. Lateralization of prey delivery by adult Caspian terns relative to age of chick

Age (weeks)	Right	Left	Ratio of R/L	P*
1	134	102	1.314	0.037
2	218	187	1.166	0.123
3	131	120	1.092	0.487
4	79	65	1.215	0.243
5	58	43	1.349	0.136

*Chi-square test for difference between right and left orientation.

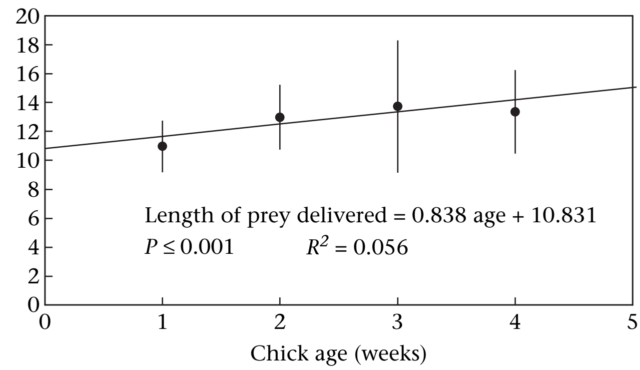

Figure 4. Mean ± SE length of prey delivered by adult Caspian terns as a function of chick age. $N = 167$ deliveries on 14 June 2005.

items were dropped during a feeding event (Fig. 6). Zero drops resulted in 6% feeding failure, a single drop increased feeding failure to 38%, and two drops resulted in 82% feeding failure.

The number of attempts and drops made by primary chicks while obtaining a prey item decreased linearly with chick age (Kruskal–Wallis test: attempts: $H_4 = 71.586$, $P < 0.001$; drops: $H_4 = 39.886$, $P < 0.001$; Fig. 7). One-week-old chicks made attempts and dropped prey items significantly more often than all other age classes (ANOVA: attempts: $F_{1,\ 4} = 15.592$, $P < 0.005$; drops: $F_{1,\ 4} = 10.411$, $P < 0.05$), after which any significant difference disappeared.

DISCUSSION

Lateralization

Caspian terns showed laterality of prey head position during delivery to chicks, with a bias towards the right. We believe that this is the first documentation of lateralization within piscivorous birds and specifically within the Laridae. Chicks almost invariably ingested the head of the prey first; thus, the orientation of prey within the bill of an adult dictates the direction from which a chick will feed. Lateralization of prey delivery may be based on brain asymmetries in visuoperceptual or motor skills that result in biased behaviours by chicks, adults, or both. We have developed a number of nonexclusive hypotheses for this finding, which are discussed below.

The discriminative ability of the right eye may be greater than that of the left eye in tern chicks. Thus, accuracy in obtaining prey would be increased when viewing an item with the right eye. A similar pattern has been reported in quail, domestic chickens and pigeons (Güntürkün et al. 2000; Valenti et al. 2003). In the domestic chick, right eye/left hemisphere dominance is attributed to an exposure of the embryonic right eye to light during the last few days of incubation, when the right eye is pressed against the shell and the left eye is positioned against the body of the chick and so remains in the dark (Skiba et al. 2002; Valenti et al. 2003; Rogers et al. 2007). In pigeons, embryonic light stimulation leads to an increase in visuoperceptual processes in the left hemisphere and a decrease in visuomotor speed in the right hemisphere (Skiba et al. 2002). It is possible that the embryonic right eye of the Caspian tern is likewise stimulated early by light, resulting in a chick bias for feeding from the right.

Chick bias could also stem from an effort to evoke less aggression from parents. This hypothesis has been proposed to explain Australian magpie bias for begging on the right side of adults (Hoffman et al. 2006). In the

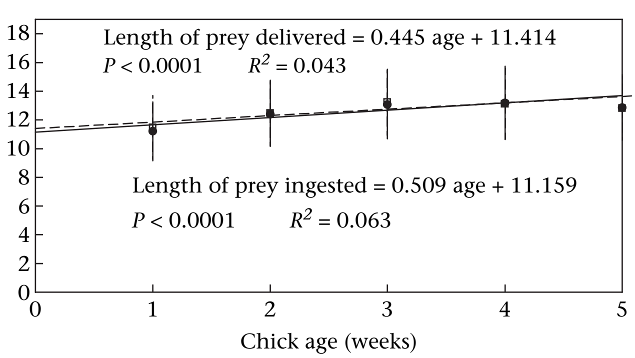

Figure 3. Estimated mean ± SE lengths of prey delivered to chicks (■) and ingested by chicks (●) as a function of chick age in Caspian terns. The broken line indicates the regression for mean length of prey delivered; the solid line is the regression for mean length of prey ingested. $N = 1215$ deliveries and 1078 successful chick feeds.

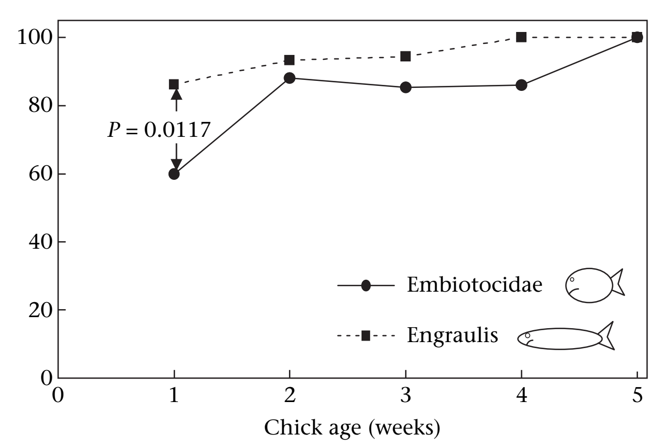

Figure 5. Percentage of delivered prey items that were ingested by Caspian tern chicks as a function of chick age. $N = 1254$ successful feeding events. P value refers to the chi-square test for the difference between the percentages of delivered engraulids and embiotocids that were consumed.

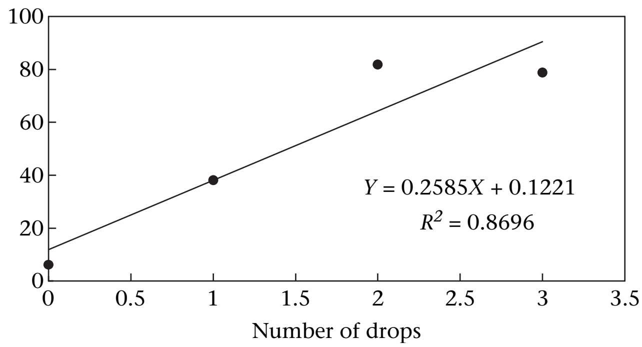

Figure 6. Percentage of feeding events that failed as a function of the number of drops by the primary chick. Feeding failure was due to kleptoparasitism by gulls, pirating by conspecifics, or the adult wandering or flying away. $N = 1494$ prey deliveries.

domestic chick, the left eye is used to scan for predators, while the left hemisphere/right eye system inhibits conspecific aggression (Dharmaretnam & Rogers 2005; Vallortigara & Rogers 2005). Chicks may simply be approaching from the 'nice' side of the adult. However, our finding that adult Caspian terns switch prey orientation from right to left before prey delivery (i.e. before a feeding attempt by a chick) suggests that adults have learned, or are genetically predisposed, to accommodate for chick asymmetry.

Alternatively, laterality may reflect an adult bias stemming from asymmetries in motor skills or visuoperceptual ability in adults. To feed small or unresponsive chicks, adults must bend down and present the prey item to the chick. Presentation and handling of prey might require refined motor skills, which in toads, domestic chicks, primates and birds of prey (Falconiformes, Strigiformes) are controlled primarily by the left hemisphere of the brain (Csermely 2004; reviewed in Vallortigara & Rogers 2005). Whatever the basis for laterality in terns, this trend does support the general right eye/left hemisphere trend for dominance in feeding (Vallortigara et al. 2005).

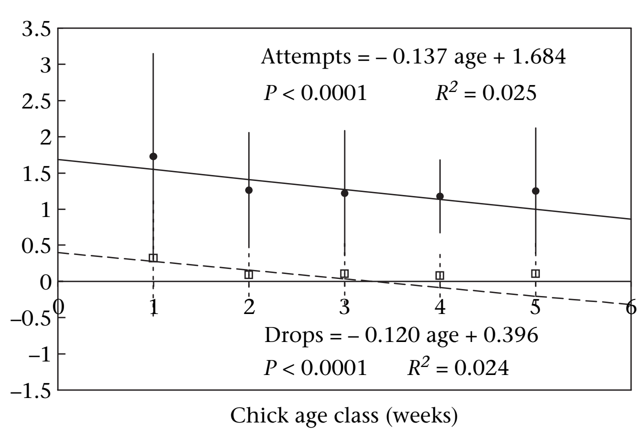

Figure 7. Mean ± SE number of attempts (●) and drops (□) made by Caspian tern chicks while obtaining a prey item as a function of chick age. The solid line indicates the regression for mean number of attempts; the broken line is the regression for mean number of drops. $N = 1343$ and 1348 prey deliveries in 2005 for attempts and drops, respectively.

Interestingly, when broken down by chick age class, significant laterality disappeared, except among feeds to 1-week-old chicks. The higher amounts of Eugraulis relative to Embiotocidae in week 1 could explain why laterality is stronger at this age. After the first week, asymmetries became less pronounced and were only significant when successive age classes were grouped together. If laterality is due to adult bias, 1-week-olds may warrant a greater degree of visual or motor control because of their small size (Fig. 2). An adult must bend down and present the prey item to 1-week-olds in a much more obvious manner than when delivering prey to older and larger chicks. In addition, older chicks consume prey items much faster than do younger chicks and they may simply allow adults no time to switch prey orientation (for a discussion of the evolution of lateralized feeding responses see Andrew 2002). Thus, feeding younger chicks may require greater motor or visuoperceptual ability and the aggressiveness of older chicks may overwhelm parental right bias.

At present, laterality may be an ancestral trait that is no longer adaptive, a by-product of ontological or physiological factors, or an adaptation to the pressures of colony life. If adaptive, lateralization may have arisen in response to the pressures of kleptoparasitism. Efficiency of prey delivery/consumption is directly correlated with feeding success; therefore, a tendency to carry prey in one orientation would be advantageous if it facilitates rapid prey consumption. A chick would know, even before an adult lands, the side from which to approach to consume the prey item.

Size and Shape of Prey

The size of prey delivered by adults and ingested by chicks increased linearly with chick age, a trend which has also been documented in Sandwich terns, *Sterna sandvicensis* (Stienen & Brenninkmeijer 2002) and roseate terns, *Sterna dougallii* (Shealer 1998). This shift in size of delivered prey can be explained by changes in the abundance of prey species and changes in adult selection criteria (Ramos et al. 1997). The onset of egg laying in terns may be related to the availability of small young prey fish to feed to their small young chicks. Yet, in our study, adult delivery in terms of prey size remained proportional to chick age within a single day, when prey availability was expected to be the same for all adults regardless of individual brood age. Thus, differential availability of prey does not completely account for the observed trend. Instead, Caspian tern adults appear to respond selectively to their chicks' energy demands (Cairns 1987) and their ability to manipulate and swallow prey of different sizes.

In terms of prey shape, chicks of all age classes consumed a larger proportion of engraulids delivered by parents relative to the proportion of embiotocids delivered, but this was most pronounced in the 1-week-old chicks (Fig. 5). Adult delivery, though, did not correspond to reduced consumption of embiotocids by young chicks. Thus, ovate embiotocids may be more difficult than fusiform engraulids for chicks to manipulate and consume, especially during the first week posthatching. A similar pattern has been observed in roseate terns: adults deliver large numbers of wide boarfish and trumpet fish to their chicks, but their chicks drop these prey items more often than they do elongate sauri and garfish (Ramos et al. 1997). Hence, adult terns appear to select prey based on relative length but not on shape. When considered from the perspective of a tern in flight, this is logical. Both ovate and fusiform prey are similarly thin when viewed from above, making them difficult to distinguish.

Five-week-old chicks experienced a decline in both size of fish and the proportion of embiotocids delivered by adults. Because of the large size and comparative dexterity of 5-week-old chicks, it is unlikely that this decline resulted from the inability of this age class to consume larger fish. Nearly all data on 5-week-old chicks were collected over a period of 4 days, so it is highly likely that availability of prey was low at this time because of external environmental factors.

Development of Prey-handling Skills

The ability of Caspian tern chicks to manipulate prey items increased with age, as measured by a decrease in the number of attempts and drops per feeding event. Although the relationship between attempts/drops and age was linear, the only significant increase in ability occurred between the first and the second weeks after hatching. One-week-old chicks are more easily captured by predators because of their small size and relative lethargy (Kirven 1969; Becker 1995), and are usually competing for food against one or two siblings, which results in a high rate of mortality during the first week posthatching (Stienen et al. 2001). Caspian tern chicks may respond to the pressures of predation and starvation by rapidly learning prey-handling skills to maximize their chances of a successful feed and, thus, increase maximal growth rate. Alternatively, predation and starvation may result in the death of all chicks that have poorer manipulation skills within the first 2 weeks after hatching.

Although it is impossible to distinguish between these two explanations in the present study, it is well accepted that tern chicks are clumsy and have a relatively high rate of food loss within the first week posthatching (Kirven 1969; Stienen et al. 2001). Qualitatively, it has also been observed that older chicks drop prey less often than do younger chicks (Ramos et al. 1997). Taken together with these studies, our findings lend support to the hypothesis that tern chicks learn to manipulate prey items and that the learning curve is relatively sharp within the first 7 days of life.

General Discussion

Our study not only adds to a growing body of research of lateralization in the wild, but it is also unique in considering lateralization as one piece of the much larger puzzle of a chick's introduction to prey. The ability to manipulate and consume prey items is intimately entwined with tern life and evolutionary history, because fitness in chicks and adults depends not only on how well parents are able to deliver prey, but also how well chicks are able to consume the prey.

Acknowledgments

We are most grateful to Willamette University and the Student Collaborative Research Program, the Mary Stuart Rogers Foundation, the M.J. Murdock Charitable Trust, Paul F. Swenson, Joel Shinn, Sam Lantz and the Columbia River Avian Predation Project.

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