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Learning the task: age-related differences in the proficiency of Black-headed Gulls kleptoparasitising Lapwings

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Abstract

How Black-headed Gulls' *Larus ridibundus* skill at kleptoparasitising Lapwings *Vanellus vanellus* improved during the course of the autumn was studied in southernmost Sweden from 1988 to 1997. Relative to adults, whose success rate remained constant, that of juveniles increased rapidly from late July to early August and more slowly thereafter. Overall success rate of adults was c. 63% and that of juveniles c. 45% based on about 5,000 attacks by each age category. In contrast to kleptoparasitism, the feeding rates of adults and juveniles did not differ when they used some other feeding methods, not even when catching flying insects on the wing about a month after the young birds fledged. This suggests that kleptoparasitism is a difficult feeding method that takes time to perfect.

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Age-related differences in foraging proficiency, with adults more proficient than juveniles and immatures, have been documented in a large number of bird species, especially fish specialists and gulls (reviews in Marchetti & Price 1989, Wunderle 1991). There are probably several reasons why these groups of birds figure prominently in such studies. First, in fish-eating birds prey-capture success is relatively easy to observe. Second, some fish-eating species, such as pelicans, like all the species of gull studied, have deferred plumage maturity which makes it possible to distinguish two or more age categories in the field. The interest in age-related differences in foraging proficiency in these groups is understandable as such differences have been suggested to explain deferred sexual maturity, i.e. why some species do not breed until their third year or later (Lack 1954, Greig et al. 1983, Burger 1988).

Two main hypotheses have been put forward to explain the existence of age-related differences in foraging efficiency. One suggests that juveniles that are poor foragers have a higher risk of dying than more efficient juveniles (Orians 1969) leaving only relatively efficient foragers in the adult population. One prediction from this hypothesis is that the variance in foraging success should be much larger in similar-aged juveniles than adults; to my knowledge this prediction has never been tested. According to the second hypothesis, adults' more proficient foraging is the result of maturation or learning processes: the various skills necessary for efficient finding and procuring of food improve gradually as the bird becomes older (Marchetti & Price 1989, Wunderle 1991).

Even though learning rather than differential mortality is probably the main factor behind adults' greater foraging proficiency, to show this conclusively one needs to study individually marked birds. This is probably the reason why this has been done in but a few studies. One example is Heinsohn et al.'s (1988) study of the group-living White-winged Chough *Corcorax melanorhamphos* in which it took up to four years for a young bird to attain the same foraging proficiency as that of adults.

In line with the learning hypothesis, it has been suggested that foraging methods differ in how difficult they are to master, and therefore in the time taken to learn them (Burger & Gochfeld 1983, Burger 1987, 1988). Here, I first test whether young gulls' foraging proficiency increases during the course of the season by using data on seasonal changes in the relative success of adult and juvenile Black-headed

Gulls *Larus ridibundus* kleptoparasitising Lapwings *Vanellus vanellus*. Changes in the adult:juvenile success ratio was used to eliminate effects of between-site and between-date variations in success rate. Kleptoparasitism appears to require considerable skill (Källander 1977, Barnard & Thompson 1985). I therefore predicted that differences in prey capture rates between adult and juvenile gulls for other feeding methods that appear less demanding should decrease much faster during the juveniles' early post-fledging period, or perhaps be absent altogether.

Methods

Data were collected in 1988–1997 near Lund, southernmost Sweden (55°42'N, 13°08'E). In much of this area, 75–90% of the land is arable, with wheat, oilseed rape and sugarbeet as the dominating crops. Flocks of both Lapwings and Black-headed Gulls use the agricultural land extensively all through the autumn. However, although Lapwings begin to flock already in early June, there are few suitable foraging sites available in the agricultural landscape until the harvest starts in August. From then on, both Lapwings and gulls are common; in certain preferred areas more than 1000 Lapwings occur regularly.

When I found flocks of Lapwings with kleptoparasitising Black-headed Gulls of both age categories (adult ≥ 2 yr, juvenile = born the same year), I recorded, for each kleptoparasitic attempt by a gull, whether the attack was successful, i.e. resulting in the gull obtaining the food (always earthworms), and the age of the gull (for plumage differences between age categories, see Cramp & Simmons 1983). Observations were made from a car with 10x40 binoculars (occasionally with a 20× spotting scope), and it was usually very easy to determine the outcome of a parasitic attack (see Barnard & Thompson 1985). Although I avoided making observations on small flocks of gulls, a certain degree of pseudoreplication exists in the material, as it was impossible to avoid recording the same individual more than once. Because of the constant mixing and often also some turnover of individuals, calculating means for individual gulls was also impossible. However, the problem of pseudo-replication no doubt applies to the majority of studies in which differences in foraging success between age categories have been quantified; the only exception I know of is the study by Hockey et al. (1989).

Data on kleptoparasitism were collected from mid-July until mid-November after which time practically all Lapwings had normally migrated. Young from the local breeding population of Black-headed Gulls start becoming independent during the last week of June (pers. obs.). However, as tens of thousands of gulls pass the area on migration (Bengtsson 1996), and stop-over for unknown periods of time, the exact age of the juveniles was unknown. It is however unlikely that any young gulls would have become independent later than by the end of July. A spread in fledging dates will of course tend to obscure the form of a possible learning curve.

To test the hypothesis that feeding methods differ in the time taken to learn them, a few sets of data were also collected in summer on feeding methods subjectively judged to require less skill than kleptoparasitism, such as searching the ground on foot or picking insects from the water surface (see Table 1). In these cases foraging efficiency was expressed as number of prey taken, or of pecks made by individual gulls during timed series of a mean length of 45 to 135 s.

Results

Using all data collected during August – November, the gulls' overall success rate in kleptoparasitic attacks on Lapwings was 53.4% (adults: 62.6%, n=5,097 attacks; juveniles: 44.7%, n=5,428; χ^2 = 338.8, d.f. = 1, P<0.001). To see if the juveniles' skill improved during the course of the autumn, the ratio of adult to juvenile success rate was calculated for each half-month. This ratio declined significantly from July to November (Spearman rank correlation, r_s=–0.976, n=8, one-tailed P<0.01; Figure 1). The ratio was particularly high in July but continued to decrease all through the autumn. As the success rate of the adults did not decline during the course of the autumn (r_s=0.45, n=8, NS), the data suggest that kleptoparasitism takes time to perfect. But what about other feeding methods? Do the juveniles' skills in using them develop equally slowly?

Table 1 compares the feeding rates of adults and juveniles in four different situations; in none of these was there any statistically significant difference between the two age groups. It is particularly noteworthy that the juveniles were as good as the adults at catching (slow-flying) small insects on the wing already on 21 July. At comparable dates (23 and 25 July), adults had considerably higher success rate than juveniles when kleptoparasitising Lapwings (66.4% vs. 25.4%, n=693 and 248 attacks, respectively; χ^2 = 124.2, d.f. =1, P<0.001).

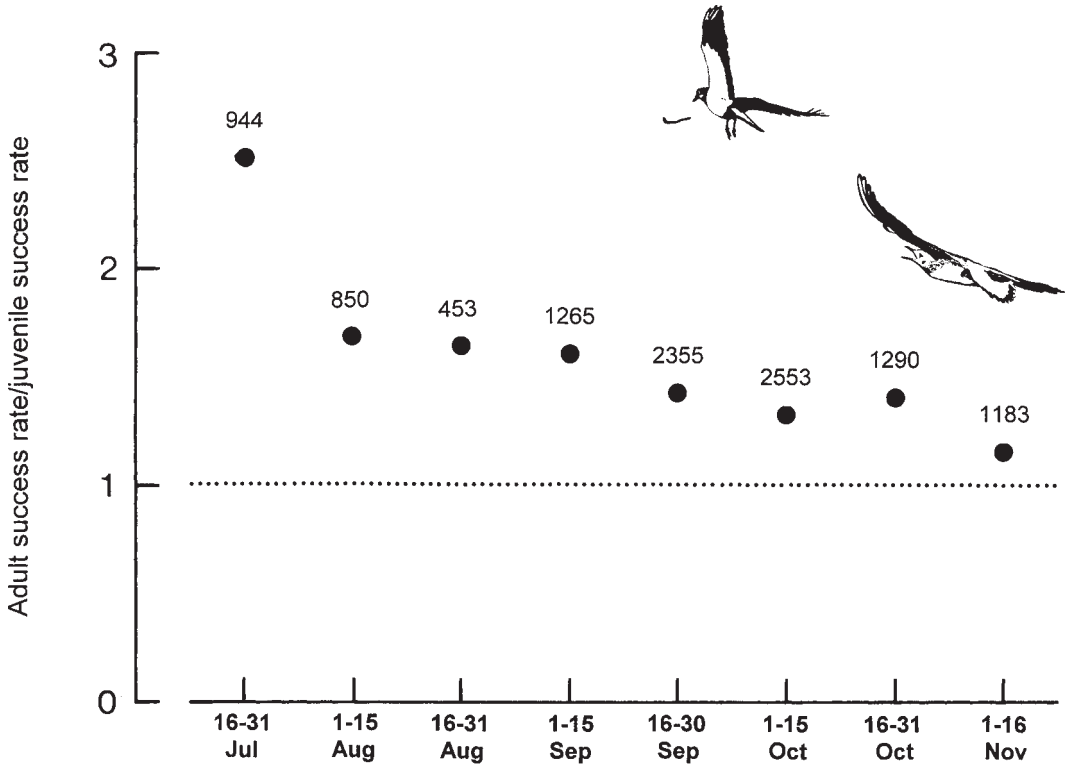

Figure1. Seasonal change in success rate of juvenile Black-headed Gulls when kleptoparasitising Lapwings in relation to the success rate of adults. Numbers above the filled circles indicate the number of attacks recorded in each half-month period and the dotted line shows equal success of adults and juveniles.
Förändringen över säsongen i unga skrattmåsars framgång vid parasitism mot tofsvipor i relation till framgången hos gamla måsar, uttryckt som kvoten mellan gamla och unga fåglars procentuella framgång. Siffrorna ovanför de fyllda cirklarna anger antalet attacker som registrerats i varje halvmånadsperiod. Den prickade linjen anger samma framgång för gamla som unga måsar.

Discussion

Stealing earthworms from Lapwings obviously is a feeding method that takes time for a young gull to master. Hesp & Barnard (1989) demonstrated that differences between the age categories in the success with which they steal earthworms from Lapwings still persist in early spring of the juveniles' second calendar year. In the present study, the adult:juvenile success ratio decreased strongly from July to August and at a slower rate during the rest of the season. Goss-Custard & Durell (1987), in their study of Oystercatchers *Haematopus ostralegus* feeding on mussels, likewise found that the largest decrease in the difference in intake rate between adults and juveniles occurred in the first autumn month and that differences thereafter declined more gradually. Whether improved foraging skills result from learning or maturation cannot be determined in a field study such as the present one but the end result would be the same.

Hesp & Barnard (1989) showed that the main reason for the juvenile gulls' lower success when kleptoparasitising Lapwings was their frequent mistiming of attacks. In my study, this was apparent throughout the autumn but was particularly striking on the two occasions in July: the juveniles appeared undetermined, even confused, and often attacked the Lapwings much too late. That the differences in success rate between the two age groups were relatively large also in late summer – early autumn is the more remarkable as the adults moult at this time. Despite often having primaries in heavy moult, with gaps in the hand wing, adults were more proficient than juveniles in kleptoparasitising Lapwings. In

Table 1. Comparison of feeding rates of adult and juvenile Black-headed Gulls when using different methods. Presented are means±SD, with sample sizes (no. of timed series) in parentheses. Differences between age categories tested with Mann-Whitney U test.
Jämförelse av gamla och unga skrattmåsars födosök i skilda situationer. Tabellen ger medeltal ± standardavvikelse, med antal tidtagna serier inom parentes. Skillnader mellan åldersgrupperna testade med Mann Whitney U test.

Date *Datum*	Feeding method *Provianteringsmetod*	Adults *Gamla*	Juveniles *Unga*	P
4 July	Searching newly cut hayfield on foot (no. of large prey/min) *Proviantering till fots på nyslagen vall (antal stora byten/min)*	1.08±0.62 (15)	1.11±1.04 (10)	0.66
20 July	Walking >15 m behind harrow (no. of pecks/s) *Proviantering till fots >15 m bakom harv (antal pickningar/s)*	0.12±0.05 (17)	0.11±0.05 (15)	0.90
21 July	Catching insects on the wing (no./s) *Flygande jakt på insekter (antal/s)*	0.24±0.05 (25)	0.22±0.05 (25)	0.09
21 July	Swimming, pecking insects* from the surface (pecks/s) *Simmande pickande insekter* från vattenytan (pickningar/s)*	0.48±0.18 (12)	0.49±0.19 (14)	0.88

* Probably surfacing chironomid pupae. *Troligen kläckande fjädermyggpuppor.*

addition to a better timing of attacks, one got the impression that adults were also more efficient in forcing Lapwings to drop the worm during aerial chases, perhaps because they flew tighter behind them than the juveniles did. However, analysis of video-recordings would be necessary to establish such differences between the age categories. Adults may also fly faster. On many occasions when a juvenile had started an aerial chase, an adult overtook the juvenile and placed itself close to the Lapwing.

Whereas for kleptoparasitism a difference in success rate between adult and juvenile gulls still remained in mid-November, no differences in foraging proficiency were found between the age categories when they were using some other feeding methods, not even very soon after the young gulls had become independent. By contrast, Frugis (1975) still found considerable differences in both success rate and prey capture rate between adult and juvenile Black-headed Gulls in November. One of the feeding methods he studied (plunge-diving) probably requires a good deal of skill (cf. MacLean 1986), but it is surprising that there were large differences between the age categories also when they were walk-feeding on mudflats. Perhaps the polychaete worms on which the gulls were feeding were both more difficult to detect and to capture than the prey taken by the gulls during my observations.

The above observations strongly indicate that feeding methods differ in the skill required to use them efficiently and that some may take considerable time to perfect. These observations may help to explain differential use of foraging sites or feeding methods by young and adult birds (Burger & Gochfeld 1983). In line with this, I noticed that juveniles in early autumn sometimes tended to give up kleptoparasitism and start using other feeding methods, such as patrolling the field on the wing (also see Hesp & Barnard 1989). Contrary to what has been found in some other studies (e.g. Moyle 1966, Monaghan 1980, Monaghan et al. 1986, Cresswell 1994), however, this is unlikely to have been because of adult physical dominance, because during kleptoparasitism juveniles attacked and supplanted adults significantly more often than the reverse (Källander

& Rosenkvist in press). Rather it was a consequence of the juveniles' lower gain from kleptoparasitism.

This study corroborates the intuitively obvious hypothesis that feeding methods differ in complexity and that a feeding method requiring much skill, such as kleptoparasitism, needs a longer period of learning than do less complex feeding methods. However, whether differences in prey capture efficiency can explain why even such relatively small species as the Black-headed Gull normally do not start breeding until their third calendar year (Cramp & Simmons 1983) is doubtful considering that no age-related differences were found for more regularly used feeding methods. It seems more likely that other aspects of foraging or parental care have a stronger influence on the age at first breeding.

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Sammanfattning

Att lära sig stjäla: skillnader i framgång mellan gamla och unga skrattmåsar vid kleptoparasitism mot tofsvipor

Åldersrelaterade skillnader i provianteringsframgång har visats hos ett stort antal fågelarter (för översikter se Marchetti & Price 1989, Wunderle 1991), inte minst hos måsar och specialiserade fiskätande arter. Anledningen till att dessa ådragit sig uppmärksamhet i detta avseende är troligen att det är relativt lätt att avgöra om ett försök till bytesfångst lyckats eller ej. Därtill kommer att många av dem ofta inte anlägger adult dräkt förrän tredje levnadsåret eller senare, vilket gör åldersseparation enkel.

Två förklaringar till varför gamla fåglar ofta är effektivare i sin proviantering än unga fåglar har framförts. Den ena går ut på att ungfåglar, som är ineffektiva, inte överlever. Den adulta populationen kommer därför att bestå av relativt effektiva prov-

ianterare. I många, kanske de flesta fall, kan emellertid gamla fåglars högre provianteringsframgång förklaras med mognads- eller inlärningseffekter, vilket visats i en studie av den vitvingade apostlafågeln *Corcorax melanorhamphos*, hos vilken det tog fyra år för en ungfågel att uppnå samma skicklighet som de adulta (Heinsohn m.fl. 1988).

Utifrån inlärningshypotesen bör man förvänta sig att olika provianteringsmetoder är olika svåra att behärska och att vissa därför tar längre tid att lära sig än andra (Burger & Gochfeld 1983, Burger 1987, 1988). I denna uppsats presenterar jag data, som visar hur unga skrattmåsars *Larus ridibundus* framgång vid parasitism mot tofsvipor förbättras under höstens lopp och jämför denna uppenbarligen svårbemästrade provianteringsmetod med några andra, för en mänsklig betraktare synbarligen enklare metoder.

Metod

Data insamlades under åren 1988–1997 i jordbrukslandskapet i sydvästra Skåne, där tofsvipor rastar i betydande antal från sensommaren och framåt. Normalt har de sista flockarna försvunnit i mitten av november och inga data erhölls efter denna tidpunkt. Flockar av tofsvipor med parasiterande måsar av båda åldersklasserna (unga födda samma år, gamla i sitt andra kalenderår eller, vanligen, äldre) studerades från bil, oftast med 10×40-kikare. För varje attack noterades den attackerande måsens ålder samt utgången av attacken, d.v.s. om måsen erhöll bytet (alltid en daggmask) från vipan eller ej (för en beskrivning av denna form av kleptoparasitism, se Källander 1977, Barnard & Thompson 1985).

För jämförelse med kleptoparasitismen insamlades också några data från andra provianteringsmetoder (Tabell 1).

Resultat

Sett över hela säsongen augusti–november var de adulta skrattmåsarnas framgång vid attackerna mot tofsvipor 62,6% (n=5097 attacker) medan de ungas var 44,7% (n=5428). För att se om de unga måsarnas framgång förbättrades med säsongens framskridande relaterades deras framgång till de gamlas (vilken förblev konstant). Detta gjordes genom att för varje halv månad beräkna kvoten mellan de gamla och de unga måsarnas genomsnittliga framgång. Som framgår av Figur1 minskade denna kvot dramatiskt från slutet av juli till augusti för att sedan minska i en lugnare takt under resten av hösten (minskningen är statistiskt signifikant, Spearman rank correlation, $r_s = -0.976$, n=8, ensvansat $P < 0.01$).

Till skillnad från kleptoparasitismen var det inga skillnader i effektivitet mellan gamla och unga måsar i de andra provianteringsmetoder, som jämfördes (Tabell 1), inte ens vid flygande insektsjakt den 21 juli, d.v.s. vid en tidpunkt då den relativa skillnaden i attackframgång mellan gamla och unga måsar vid tofsvipeparasitism uppgick till 41%.

Diskussion

Det är uppenbart att det tar tid för unga skrattmåsar att förbättra sin förmåga att kleptoparasitera tofsvipor. Hesp & Barnard (1989) fann skillnader mellan ålderskategorierna ännu i början av våren. De visade också att det mesta av skillnaderna förklarades av att de unga måsarna antingen initierade attackerna för tidigt eller för sent. Troligen är också andra faktorer inblandade, t.ex. attackerar möjligen gamla måsar intensivare och flyger närmare tofsvipan under luftjakter, men för att avgöra detta krävs analyser av videoupptagningar. Det är dock intressant att notera att de adulta under tidig höst, då handvingen ofta är under betydande ruggning, ändock hade avsevärt högre framgång än de unga.

I en studie av strandskator *Haematopus ostralegus* erhöll Goss-Custard & Durell (1987) ett likartat resultat: minskningen i skillnaderna mellan gamla och unga strandskators intag av musslor var störst den första höstmånaden för att sedan avta mera gradvis.

Resultaten av denna studie visar att vissa provianteringsmetoder är svårare än andra att bemästra och kan förklara varför gamla och unga fåglar under stundom använder olika födosöksplatser och/eller födosöksmetoder (Burger & Gochfeld 1983).