Sibling conflict in Montagu's harrier *Circus pygargus* during the post-fledging period in south-east Poland

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Abstract Sibling rivalry was studied in 13 broods (total of 37 fledglings) of Montagu's harrier *Circus pygargus* from a breeding site in south-eastern Poland. The oldest sibling in broods tended to monopolise food in the nest and in the air (both in terms of numbers and estimated overall biomass). The proportion of food transfers taking place in the air tended to increase as the fledglings aged. Aggressive interactions between flying offspring were observed only during aerial food transfers. Of 730 aerial food transfers, 57 (7.8%) fell to the ground as a result of sibling competition. Juveniles that did not obtain prey from their parents due to sibling rivalry were sometimes seen trying to capture nearby passerines. Adults rarely demonstrated preferential feeding of the youngest offspring. The larger the brood, the longer lasting sibling conflicts over prey. Success at obtaining prey during aerial food transfers was correlated with spatial distribution of offspring prior to a given feeding event. The chicks hierarchy established during the nestling stage was preserved over the post-fledging period, which allowed the oldest juveniles to start migrating in good condition [*Acta Zoologica Sinica* 51 (5): 790 – 796, 2005].

Key words Montagu's harrier, Circus pygargus, Sibling conflict, Sibling competition, Post-fledging period

波兰东南部乌灰鹞在雏鸟出羽后期的同窝雏间冲突

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摘 要 通过对波兰东南部的 13 巢乌灰鹞(Circus pygargus), 37 只雏鸟观察,对同窝雏鸟间的竞争进行了研究。无论是在食物的数量或者生物量上,早孵出的雏鸟占有空中喂养与巢内喂养的食物源的绝对优势。空中学习捕食的食物量占喂养食物量的比例随着雏鸟年龄的增长而增加。雏鸟在空中喂养中的攻击行为通过对空中食物传递进行研究。在 370 次的食物传递中,由于雏间竞争而引起的落地食物的比例 57 次(7.8%)。由于雏间竞争而不能获得亲鸟喂养的幼鸟有时捕食周围的雀形目小鸟。亲鸟很少喂养较小的雏鸟。窝雏数越大,雏鸟间对食物的争斗持续时间越长。空中食物传递中捕食的成功率与雏鸟的空间分布相关。这种建立在雏鸟早期的等级制一直持续到雏鸟的出羽后期,从而保证早出雏具备开始迁徙的良好身体条件[动物学报 51(5):790-796,2005]。

关键词 乌灰鹞 雏间争斗 雏间竞争 雏鸟出羽后期

Most studies on sibling rivalry, focus on the nestling stage, when chicks are totally dependent on prey delivered to their nest by parents. Sibling aggression (Edwards and Collopy, 1983; Simmons, 1991) often has fatal consequences (siblicidal brood reduction: Newton, 1979; Poole, 1982; Forbes, 1991; Simmons, 1988, 1997; Ellis et al., 1999; Vinuela, 1999). Other aspects of sibling rivalry on raptors such as impact on the growth rate, the influ-

enced prey size, establishment of food distribution, hierarchies among the nestlings, sibling negotiations, and parent feeding preferences over the period when fledglings stay on the nest are well known (Steidl and Griffin, 1991; Anderson et al., 1993, Gerhard et al., 1997; Roulin, 2001). However, as pointed by Mock and Parker (1997), sibling conflicts do continue after fledging. Because published accounts of postfledging rivalry in birds are only anecdotal (e.g., Ce-

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ballos and Donazar, 1990; Bustamante, 1995; Mock and Parker, 1997), detailed studies of the phenomena based on long term observations are need especially in nidicolous birds.

The first purpose of the present work was to examine quantitatively and qualitatively sibling conflicts during the post-fledging dependency period in Montagu's Harrier. No such studies has been conducted for any bird of prey despite a longstanding recognition for the need (Mock and Parker, 1997). My second goal was to determine roles in the post-fledging sibling competition. The third goal was to determine if social hierarchies established in the nestling stage were preserved during the post-fledging period, and if so what factors influence such behavior. The third goal is to determine a parental role in the post fledging sibling competition. The third point is to elicit the answer whether the established in nestling stages size and motor skills hierarchy is preserved, and if yes what makes it maintained during the post fledging period.

1 Study area and methods

Montagu's harriers Circus pygargus are medium-sized, relatively long living raptors that are known to exhibit facultative siblicide (Krogulec*). The species is a highly opportunistic predator on such taxa as small mammals, passerines and orthopterans (Cramp and Simmons, 1980; Karwat**; Butet and Leroux, 1993; Giacchini and Pandolfi 1994; Salamolard et al., 2000; Kitowski, 2001). Field observations were performed from 1989 to 1992 on a population of 20 - 42 breeding Montagu's harriers pairs (Krogulec*; Kitowski[@]; Buczek and Buczek, 1996; Kitowski, 2002) nesting in saw sedge Cladium mariscus in the area of calcareous peat bogs near Chelm (51°08′ N, 23°37′ E), southeaster Poland. Shortly before the presented post-fledging studies, productivity of harriers wase studied on area of peat bogs. In 1985 - 1988 the harriers laid on average: 4.15 eggs, range: 1 - 6 eggs (n = 125 clutches). Breeding success was 2.61 juv./brood with flying fledglings (n = 84) and 1.72 juv./breeding pair (n= 127) (Krogulec*). Adults were not tagged due to the risk of abandoning the broods (Pandolfi, 1996; Wiacek***), but individual features of plumage made it possible to distinguish approximately 90% individuals.

To facilitate recognition of plumage, sketches and drawings were made, as well as photos taken. A total of 37 fledglings from 13 families were individually marked with Saflag® foil patagial tags providing temporary identifications. These were comprised of five families of two fledglings each, six families of three, one of four, and one family of five fledgings. The tagging procedure was described in details elsewhere (see: Kochert et al., 1983; Bustamante, 1990; Kitowski, 2001). Age and sex of juveniles was estimated while examining nests during hatching, and double-checked late in the nestling period using measurements of 1st and 5th primaries (Krogulec*). Sex was determined from the iris color (brown-grey in young males, chocolate in young females) (Krogulec, 1992; Kitowski, 2001; Arroyo, pers. comm.). Field studies consisted of 12-hour observation (8:00-20:00) for each of the families, and were performed every 1 to 4 days.

Observations commenced with the first juvenile flights and continued until the birds began leaving the breeding areas with the start of the autumnal migration. The total number of observation hours was 1 770 hours (in average: 136 h for each of 13 families). Offspring remained under parental care 23.6 ± 3.6 days (n = 42, range = 17 - 31 days) after fledging (Kitowski, 2002). For convenience, the dependency period was divided into 16 two-day segments. Observations began 2-3 days before the expected date of the first flight (late June- early July).

For the purpose of this, families with 2, 3, 4, and 5 fledglings were denoted as F2, F3, F4, and F5 families, respectively. Juveniles are represented by an alphanumeric code as follows: a4 stands for the oldest from a family of 4 juveniles, while symbols a5, e5 are the oldest and the youngest siblings, respectively, in a F5 family. Basic prey of Montagu's harrier in study area during post-fledging period are small mammals, chiefly Microtus arvalis (79% by estimated mean mass, see below). Other important prey are passerines, mainly Acrocephalus sp., Moticilla sp., and Passer sp. (18% of total biomass), and orthopterans, mainly great grey bush cricket Tettigonia viridissima (2% of total biomass). Other preys are small amphibians and reptilians (1% of total biomass). These data were obtained from pooled

^{*} Krogulec J. 1992. Breeding ecology of Montagu's harrier Circus pygargus on calcareous marshes near Chelm. Unpublished Ph.D Thesis, Univ. of Maria Curie-Sklodowska. Lublin, Poland (In Polish).

^{**} Karwat M• 1990. Food composition of Montagu's harrier Circus pygargus during breeding on calcareous marshes near Chelm. Unpublished M. Sc. thesis, Univ. of Maria Curie-Sklodowska. Lublin, Poland (In Polish).

[@] Kitowski I, 1994. The post-fledging period ecology of Montagu's harrier Circus pygargus on calcareous marshes near Chelm. Unpublished Ph.D Thesis, Univ. of Maria Curie-Sklodowska. Lublin, Poland (In Polish).

^{***} Wiacek J. 1998. Pre-laying period ecology of Montagu's harrier *Circus pygargus* on the calcareous marshes near Chelm. Unpublished Ph. D. Thesis, University of Maria Curie-Sklodowska. Lublin (In Polish).

data from pellets analysis (Karwat**; Kitowski[@]; Kitowski, 2001).

The mammal and bird biomasses were calculated as 20 g each (as described by Pucek, 1984; Busse, 1990). The estimated mean for Orthopterans (0.7 g) was determined by weighing freshly captured adults of great grey bush cricket *Tettigonia viridissima* (Kitowski, 2001). The reptile figure of 20 grams came from specimens of the common lizard *Lacerta agilis* (following Juszczyk, 1974).

One behavioral term needs defining: "mantling" behaviour, as used here, consists of a juvenile covering the prey with its body and thereby screening it from the view of siblings. Frequencies of various activities were compared with χ^2 test with Yates' correction. Trends were ascertained using Spearman rank correlation. Differences in time duration between the class size of broods were compared with Kruskal-Wallis ANOVA. The results are presented as mean \pm SD (Sokal and Rohlf, 1981; Fowler and

Cohen, 1992).

2 Result

2.1 Competition of juveniles in the early post-fledging period

Of 1 584 observed prey deliveries, all fell into one of three classes: (a) at the nest (n=743, 46.9%), (b) on the ground (n=111, 7.0%), or (c) in mid-air (n=730, 46.1%). In the first three weeks of the post-fledging period, 743 prey items were delivered to the nest, with 718 of them consumed there, 36 dragged away, and 11 carried away by the juveniles (Table 1). Of these 47 prey removal events, a-siblings escaped with the prey 33 times (70.2%), while all 14 other prey were carried off by b-siblings. Siblings c, d, and e never escaped the nest with prey. The prey, all of which were voles, were removed at different rates by e- and e-siblings (e) and e never escaped the nest with prey. The prey, all of which were voles, were removed at different rates by e- and e-siblings (e) and e never escaped the nest with e0.01) and its biomass (e) and e1 and e1 and e2 and e3.

Table 1 Incidence of prey dragged out of the nest, and dragged into the nest during the early post-fledging period

	Prey of a-siblings	Biomass prey (g)	Prey of b-siblings	Biomass prey (g)
Prey dragged away out of the nest	27	540	9	180
Prey carried away into the nest	6	120	5	100
Total	33	660	14	280

2.2 Prey and biomass distribution during aerial food transfers

Juveniles successfully obtained prey in mid-air 618 (84.7%) of 730 times, comprising approximately 9 099 g of estimated biomass. The proportion of food transfers taking place aloft increased as the fledglings aged (r = 0.967, n = 16, P <0.001). For 148 aerial food transfers observed for two-chick broods, the elder sibling (a2) received more than half of the prey (58.1% by count, 60.2% by estimated mass, $\chi^2 = 3.89$, df = 1, P < 0.05). Similarly, biomass m = 2 314 g unequally favored the elder sibling ($\gamma^2 = 15.4$, df = 1, P < 0.01). In F3 families, of 281 aerial food transfers with a total biomass of 4 172 g, a3, b3, and c3 siblings secured prey 124, 84, and 73 times, respectively, which contributed to 44.1%, 29.9%, and 26.0 % of prey. Distribution of prey by numbers ($\chi^2 =$ 15.4, df = 2, P < 0.01) and biomass (a3 = 42.8%, b3 = 30.1%, c3 = 27.1%) ($\chi^2 =$ 173.1, df = 2, P < 0.01) were not equal for siblings by age. In F4 families, 97 aerial food transfers were observed. Siblings a4 secured 40.2% of prey, while b4 siblings secured 24.7%, c4 siblings secured 9.6%, and d4 siblings secured only 5.5% of all prey. In this case, unequal distribution of prey by

numbers ($\chi^2 = 13.6$, df = 3, P < 0.01) led also to unequal distribution by biomass (m = 1216 g) and yielded values of 42.9%, 24.9%, 18.6%, and 13.6% for siblings of type a4, b4, c4, and d4, respectively ($\gamma^2 = 239.9$, df = 3, P < 0.01). In the F5 family, 92 aerial food transfers of prey were noted. The percentage of prey secured during aerial food transfers by a5, b5, c5, d5, and e5 siblings reached 42.4%, 19.5%, 16.3%, 11.9%, and 9.8%, respectively. Both the distribution of prey procured by number ($\chi^2 = 31.48$, df = 4, P <0.01) and by biomass (1 397 g total divided as follows: a5 = 4.8%, b5 = 17.5%, c5 = 17.4%, d5 = 10.2%, e5 = 10.1%) were found different from the expected ($\chi^2 = 572.9$, df = 4, P <0.01).

In 364, nearly half (49.9%) of 730 of the aerial pursuits observed, the siblings' original starting perches were known. When these perches differed in height (high bushes and hay cones vs. ground), the successful sibling tended to launch from the higher site (64.8% of 176 cases, $\chi^2 = 15.36$, df = 1, P < 0.01). For the remaining 188 events, all rivals started from the ground before the aerial food transfers, in which case most (65.4%) prey were obtained by siblings whose position had the clearest view

of the arriving parent ($\chi^2 = 17.89$, df = 1, P < 0.01).

2.3 Sibling aggression and struggles over prey

A total of 175 prey items were actively contested after one fledgling had obtained possession from the parent: $137\ (78.3\%,\ n=175)$ of these involved aerial attempts to tear $(n=161\ \text{trials})$ the prey item from the sibling's talons in the air (Table 2). Such prey were almost surely small mammals (*Microtus* sp.), the lone exception being a cricket that broke apart during the struggle. Only once did the youngest sibling (c5) try to take prey from the eldest (a5); it lost the battle. Only 9 times was prey stolen from the original possessor. Prey stealing attempts were most successful by a3 and c3 siblings. Other siblings were less efficient: a2-1 prey and b5-1 prey. Young females attacked effectively retrieved 6 prey from host

birds, while males only succeeded in stealing 3 prey. Aerial prey pirating bouts lasted on average 15.5 \pm 8.0 sec. (range 4 to 32 sec.) and were more prolonged in the brood of five juveniles, all of which were capable of flight (Table 3). In general, struggles over prey items differed sharply in duration between the four class size of broods (Table 3) (Kruskal -Wallis ANOVA: H = 81.5, df = 3, P < 0.001).

Table 2 Occurrence of pulling prey successfully obtained from parents during aerial prey transfer

D	Number of prey	Number trials pulling prey		
Prey		1	2	3
Small mammals	136	117	14	5
Orthopterans	1	1	_	_
Total	137	118	28	15

Table 3 Incidence of pirating prey (n = 137) between young Montagu's harriers

Families	F2	F3	F4	F5
Number observation	33	34	27	43
Time duration	$6.97 \pm 2.0 \text{ sec.}$	$12.06 \pm 6.5 \text{ sec.}$	$17.4 \pm 3.9 \text{ sec.}$	23.7 ± 4.9 sec.
Range	4 - 10 sec.	3 - 32 sec.	9-23 sec	10 - 32 sec.

I observed 19 bouts of cartwheeling; these resulted from two juveniles simultaneously catching prey dropped by an adult. In 11 of 19 cartwheeling struggles, the two youngest juveniles were involved (b or c and d or e-siblings). Whereas 8 cartwheeling flights involved young birds more diversified in age. Whirl flights were not observed in F2-families. Three prey were stolen from siblings in whril flight context. During observation 379 dives or pushing of siblings performed by 29 offspring were seen; 363 such attacks (96%) took place in the feeding context (when delivered prey by adults was present close group of juveniles): $\chi^2 = 317.7$, df = 1, P <0.01. While attempting to take over the dropped prey, 221 dives or pushing were observed. Remaining 142 attacks took place after aerial food pass, out of which 134 ended in failing to obtain the prey from the adults and 8 was a response to other siblings begging. Difference in the frequency of attacks performed prior to and following aerial food pass, was significant ($\chi^2 = 21.3$, df = 1, P < 0.01). Young males performed more frequently dives or pushing on

their siblings compare to young females (57.6% vs. 43.4 % of 379 events, $\chi^2 = 8.57$, P < 0.034). With progress of the season, the number of attacks kept increasing (r = 0.391, n = 16, P < 0.01). Generally speaking, siblings having received prey, try to escape into the high grass to eat prey, and only in 39 cases their behaviour on the ground could be observed. For siblings that were defending the prey on the ground, 32 events of 'mantling behaviour' were recorded ($\chi^2 = 16.02$, df = 1, P < 0.001). Sessions of "mantling" lasted on average 22.0 ± 7.0 sec., and ranged from 11 to 38 sec. (Table 4). There were significant differences noted between the duration of mantling sessions in four brood size classes (Kruskal-Wallis ANOVA: H = 13.96, df = 3, P < 0.01) (Table 4). None of the observed attempts to extort prey on the ground was successful. Fledglings that loose struggles over prey from their parents were also sometimes seen trying unsuccessfully to capture nearby passerines (n = 31) shortly after food transfer.

Table 4 Duration and number observed "mantling behaviour" sessions

Families	F2	F3	F4	F5
Number cases	7	16	4	5
Time duration	$17 \pm 6.0 \text{ sec.}$	$21 \pm 6.0 \text{ sec.}$	$24 \pm 5.0 \text{ sec.}$	34 ± 4.0 sec.
Range	11 - 28 sec.	11 - 30 sec.	19 - 30 sec.	29 - 38 sec.

2.4 Successful aerial food pass vs. sibling competition

As many as 112 (15.3%, n=730) aerial food transfers ended in failure. Of these, about half: n=57 (7.8%, n=730) fell to the ground when attempted receptions by the brood's youngest members (23 by b2, 32 by c3, and one each by d4 and e5 sib.) were spoiled by interference by senior siblings. Of these prey items, only 49% were retrieved by juveniles (n=22) or adults (n=6). The other 29 prey were lost. When a parent recovered a dropped item, it tried again to pass it to a brood members. The other half of failed aerial food transfers n=55 (7.5%, n=730) resulted from poor catching abilities or successful kleptoparasitism by non-sibling juveniles.

2.5 Parental behaviour in relation to sibling competition

Three actions by Harrier parents seemed effective in mitigating sibling rivalry for food, namely: 1) one short-term (246 minutes) division of broad members in a F5 family (described in details elsewhere, see (Kitowski and Czochra, 1997). The brood was spatially divided into two separated subgroups, which were kept at a 200 - 250 m distance from each other. The adult male was feeding only 3 flying juveniles, whereas the female kept feeding the other 2 juveniles. Such a brood division was not observed at any other nest; 2) Selectively feeding the youngest juveniles (four in F3 and two in F5 families when their more senior siblings seemed to be deliberately evaded; 3) In the late post-fledging period (52.0 \pm 4.2 days after hatching, n = 12, range: 48 - 61 days after hatching) adults performed dives on begging juveniles. Nearly all such harassing (83%) was directed at on the oldest sibling in brood.

3 Discussion

The achievement of sustained flying ability and its associated emancipation from the nest site does not terminate sibling competition in Montagu's harrier broods studied in SE Poland such attacks are acute and sometimes fatal (Krogulec*). Sibling rivalry is sometimes milder during the post-fledging period in other populations of Montagu's harrier (Pandolfi and Giacchini, 1990; Arroyo et al., 2002; Pandolfi, pers. comm.) as well as in other raptors (Ceballos and Donazar, 1990). In many other raptors sibling rivalry is also merely manifested (Bustamante and Hiraldo, 1990; Bustamante, 1990). Such behaviour in studied Harriers may be attributed to a number of factors that generate conflicts between maturing raptor siblings. Reduced parental investment throughout the post-fledging dependency period is the most significant stimulating the conflict. This because as juveniles aged there is reduction in both the number of feeding sessions and the delivered biomass (Bustamante, 1993; Bustamante, 1995; Kitowski, 2000a; Kitowski, 2002).

Another factor that may contribute to sibling conflicts after leaving the nests is small size of prey: as it happened already at the nestling stage (Mock, 1985; Anderson et al., 1993). Other factors stimulating sibling conflict is simple asynchrony in nestling development. The strongly pronounced hierarchy of size is deeply rooted in asynchronous hatching and enhanced later by sex dimorphism (Newton, 1979, 1986; Village, 1990; Anderson et al., 1993; Vinuela, 1999). Senior sibs have (almost) certainly been enjoying disproportionate shares of the pre-fledging food because of their superior motor skills, size and strength (Mock, 1987; Mock and Paker, 1997). This leads to a diversification of offspring age when leaving the nest, and mass and size at the time of the first flights (Arroyo et al., 2000; Kitowski, unpublished data). The advantage of the older siblings in broods is significant already at the nestling stage and results in strong benefits from control of feedings (Arroyo et al., 2002).

Strongly manifested sibling competition is a significant factor influencing adults to deliver the prey via aerial food transfers. Even slight physical size separation may well protect delivering adults from injury from competing sibs (Fernandez and Azkona, 1994). The increasing use of aerial food transfers, which typically dominates the second post-fledging period, has the effect of increasing the skew in prey distribution toward senior siblings without any escalation of overt sibling aggression. That, in turn, extends and consolidates the intra-brood size hierarchy, created by hatching asynchrony and reinforced behaviourally throughout the nestling stage, effectively ensuring that it lasts through the entire dependency period. As a result, the first-hatching chicks are more likely to reach the point of full independence in peak physical condition (e.g., Simmons, 1988). Disrupting the mass and size hierarchy during the post-fledging period in broods of the Montagu's harrier could reduce the certainty of an optimal growth in the firsthatched fledgling and may substantially affect the ability of such individuals to prepare for the challenges of the migration, which begins in mid-August (Kitowski[@]; Spaar, 1996).

Though numerous studies have shown that most of adult birds appear indifferent to sibling rivalry during the nestling stage (Mock and Parker, 1997), some species demonstrate preferential feeding of the smallest chicks by deliberately skipping the others (Braun and Hunt, 1983; Ferguson and Sealy, 1983, Gottlander 1987; Vinuela, 1999). A few incidents

observed for Montagu's harrier during the post-fledging dependency period suggests that this species may be flexible and parental favourism may be latent in that regard. Only ospreys Pandion haliaetus and Bonelli's eagle Hieraaetus fasciatus were observed in the post-fledgling period to perform "beak to beak" feeding (Bustamante, 1995; Real et al., 1998). Adults of these raptors sometimes direct the prey to a selected sibling even when it is capable of flying. This serves to reduce the sibling tensions during a feeding session. It seems that juvenile's predation toward passerines after failing to receive from an adult prey also serves to reduce the tension between juveniles, which in the face of high cost of being hurt during the aggressive interactions, proves to be an important adaptation. Such behaviour was also noted in hacked juveniles of Montagu's harrier in Spain (Pomarol, 1994). During this post-fledging period juveniles also hunt insects but not efficiently enough provide for their needs (Arroyo et al., 2002; Kitowski, 2003). It is quite likely that low cost sibling tensions that result from the buffering adaptation, and partially explains the behavioural indifference shown by Montagu's harrier adults in response to sibling conflicts (Fujioka, 1985). By contrast the adults of a selected other species actively intervene in competition between siblings (Spellerberg, 1971).

The short duration of aggressive interactions, limited solely to the periods of food distribution constitutes small proportion of the time budget of Montagu's harrier juveniles. Similar is known in other raptors (Lett and Bird, 1987; Bustamante, 1990). Family tension can be reduced by kleptoparasitic behaviour and adoption of unrelated juveniles (Bustamante and Hiraldo, 1993; Kitowski, 2000b, 2001). This proclivity to purchase birds with prey is sometimes reoriented towards other neighbouring families of conspecifics and sympatric Marsh harriers *Circus aeruginosus*. However, kleptoparasitic behaviour of young Montagu's harriers is limited by their flying skills (Kitowski, 2001).

Numerous studies conducted on sibling competition in the nestling period have indicated that the oldest chicks are fully capable of monopolising a favourable position before each feeding session this, in turn, enables them to monopolise prey delivered to the nest (Bengtsson and Ryden, 1983; Gottalander, 1987; Vinuela, 1999). This ability seems to also be function after leaving the nest in Montagu's harrier fledglings. Better flying skills contribute to this advantage. The advantage, however, of older juveniles may be controlled to a degree by adult birds extending the home ranges of offspring (i.e. leading individual young at field). This practice seems significant in developing foraging skills and initiating of dispersal of

their young (Bustamante and Hiraldo, 1989; Bavoux et al., 1998; Kitowski, 2003).

Sibling conflict does not appear to be an important element initiating dispersal of Montagu's harrier offspring. Migratory pressure is the major initial factor for dispersal that curtails family conflicts, as has been demonstrated for other non sedentary raptors (Bustamamante and Hiraldo, 1990). It should be noted, however, that in sedentary (i.e., non migratory) species, intra-brood aggression, in particular that demonstrated by a dominant juvenile is a factor initiating limited dispersal of other brood members, to which the same function may be attributed during the post-fledging period as brood reduction plays in the nestling period (i.e., making the dominant juvenile beneficial in terms of access to food delivered by parents) (Strickland, 1991).

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参考文献 (References)

Anderson DJ, Budde CC, Apanius V, Martinez-Gomez JE, Bird DM, Weathers WW, 1993. Prey size influences female competitive dominance in nestling American kestrels Falco sparverius. Ecology 74: 367 – 376.

Arroyo B, Mougeot F, Bretagnolle V, 2000. Colonial breeding and nest defence in Montagu's harrier Circus pygargus. Behav. Ecol. Sociobiol. 50: 109 – 115.

Arroyo BE, de Cornulier TH, Bretagnolle V, 2002. Parental investment and parent-offspring conflicts during the post – fledging period in the Montagu's harrier. Animal Behav. 63: 235 – 244.

Bavoux C, Burneleau G, Nicolau-Gillaumet P, Picard M, Sahuc C, 1998. Dependence and emancipation in juvenile marsh harriers Circus a. aeruginosus. In: Chancellor RD, Meyburg BU, Ferrero J ed. Holarctic Birds of Prey. Berlin, Germany: Adenex-WWGBP, 91 – 100.

Bengtsson H. Ryden O. 1983. Parental feeding rate in relation to begging behaviour in asynchronously hatched broods of the great tit *Parus major*. Behav. Ecol. Sociobiol. 12: 243-251.

Braun BM, Hunt GL, 1983. Brood reduction in black-legged kittiwakes. Auk 100: 469 – 476.

Buczek T, Buczek A, 1996. Calcanerous Marshes of Chelm Region. Lublin: IUCN Poland (In Polish).

Busse P, 1990. Small Zoological Dictionary: Birds. Warsaw, Poland: Wiedza Powszechna (In Polish).

Wiedza Powszechna (In Polish).
Bustamante J. 1990. Ecological factors of the emancipation period of the Falconiformes. Ph.D Thesis. Facultet of Science. University Autonoma de Madrid. Spain (In Spanish).

Bustamante J. 1993. Post-fledging period and development of flight and hunting behaviour in red kite *Milvus milvus*. Bird Study 40: 181 – 188.

Bustamante J, 1995. The duration of the post-fledging dependence period of osprey *Pandion haliaetus* at Loch Garden, Scotland. Bird Study 42: 31 – 36.

- Bustamante J. Hiraldo F. 1989. Post-fledging dependence and maturation of flight skills in the black kite *Milvus migrans*. Bird Study 36: 199 204.
- Bustamante J. Hiraldo F. 1990. Factors influencing family rupture and parent-offspring conflict in the black kite *Milvus migrans*. Ibis 132: 58-67.
- Bustamante J. Hiraldo F. 1993. Adoptions of fledglings by black and red kites. Anim. Behav. 39: 805-806.
- Butet A, Leroux A, 1993. Effect of prey on predator's breeding succes. A 7-year study on common vole *Microtus arvalis* and Montagu's harrier *Circus pygargus* in west France marsh. Acta Ecologica 14: 857 865.
- Ceballos O, Donazar JA, 1990. Parent-offspring conflict during the post-fledging period in Egyptian vulture Neophron percnopterus. Ethology 85: 225 – 235.
- Cramp S, Simmons RKEL, 1980. The Birds of Western Palearctic, the Middle East and North Africa. Vol. []. Oxford. UK: Oxford University Press, 132 143.
- Edwards TC, Collopy MW, 1983. Obligate and facultative brood reduction in eagles: an examination of factors that influence fratricide. Auk 100: 630 635.
- Ellis DH, Whitlock PL, Tsengen P, Nelson RW, 1999. Siblicide, splayed-toeds-flight and grappling in the saker falcon. J. Raptor Res. 33: 164 – 167.
- Ferguson RS, Sealy SG, 1983. Breeding ecology of the horned grebe Podiceps auriatus, southwestern Manitoba. Can. Field. Nat. 97: 401 – 408.
- Fernandez C, Azkona P, 1994. Aerial food transfers as demand behaviour in the marsh harrier. J. Field. Ornithol. 65: 109 114.
- Forbes LS, 1991. Hunger and food allocation among nestlings of facul-
- tatively siblicidal ospreys. Behav. Ecol. Sociobiol. 29: 189 195. Fowler J. Cohen L. 1992. Statistics for Ornithologists. Guide 22. UK: BTO.
- Fujioka M, 1985. Sibling competition and siblicide in asynchrously-hatching broads of the cattle egret *Bulbucus ibis*. Animal Behav. 33: 1 238 1 242.
- Gerhard RP, Gerhard DM, Vasquez MA, 1997. Siblicide in swallow-tailed kites. Wilson Bulletin 109: 112 120.
- Gottlander K, 1987. Parental feeding behaviour and sibling competition in the pied flycatcher *Ficedula hypoleuca*. Ornis Scandinavica 18: 269 – 276.
- Giacchini P, Pandolfi M, 1994. Feeding habits of Montagu's harrier Circus pygargus in Central Italy. In: Meyburg BU, Chancellor RD ed. Raptor Conservation Today. Berlin, Germany: WWGBP/The Pica Press, 117–122.
- Juszczyk W, 1974. Amphibian and Reptilian of Our Country. Warsaw, Poland: PWN (In Polish).
- Kitowski I, 2000a. The food of Montagu's harrier *Circus pygargus* during the post-fledging period on calcareous marshes near Chelm. In: Letowski J ed. Natural Values of Chelm Landscape Park and Its Surroundings. Lublin, Poland: UMCS, 177 182 (In Polish).
- Kitowski I, 2000b. A case of natural adoption in Montagu's harrier *Circus pygargus* in the period of emancipation. Notatki Ornitologiczne 41: 86 88 (In Polish).
- Kitowski I, 2001. Intra-and inter specific kleptoparasitism in Montagu's harrier *Circus pygargus* during the post-fledging period. Biota 2: 137 145.
- Kitowski I. 2002. Behaviour of Montagu's harrier juveniles *Circus py-gargus* during the post-fledging dependency period in SE Poland. Berkut 11: 201 207.
- Kitowski I, 2003. Differences between social hunting and non-social

- hunting of juvenile Montagu's harrier *Circus pygargus* in the post-fledging dependence period. Ornitologischer Anzeiger 42: 147 152.
- Kitowski I, Czochra K, 1997. The case of brood division in Montagu's harrier Circus pygargus during the post-fledging period. In: Puszkar T, Puszkar L ed. Current Trends in Ecology. Behavioural ecology. Lublin, Poland: UMCS. LTN, 139-141 (In Polish).
- Kochert MN, Steenhof K, Moritsch MQ, 1983. Evaluation of patagial markers for raptors and ravens. Wildl. Soc. Bull. 11: 271 – 281.
- Lett DW, Bird DM, 1987. Post-fledging behavior of American Kestrel in southwestern Quebec. Wilson Bull. 99: 77 82.
- Mock DW, 1985. Siblicidal brood reduction: the prey-size hypothesis. Am. Nat. 125: 327-343.
- Mock DW, 1987. Siblicide, parent-offspring conflict, and unequal parental investment by egrets and herons. Behav. Ecol. Sociobiol. 20: 247 256.
- Mock DW, Paker GA, 1997. The evolution of sibling rivalary. Oxford, UK: Oxford University Press.
- Newton I, 1979. Population Ecology of Raptors. Berkhamsted, UK: Poyser.
- Newton I, 1986. The Sparrowhawk. Calton, UK: T & AD Poyser.
- Pandolfi M, 1996. Play activity in Montagu's harrier $Circus\ pygargus$. Auk 113: 935 938.
- Pandolfi M, Giacchini P, 1990. First record of juvenile-juvenile kleptoparasitism in Montagu's harrier *Circus pygargus*. Avocetta 14: 74-75 (in Italian).
- Pomarol M. 1994. Releasing Montagu's harrier *Circus pygargus* by the method of hacking. J. Raptor. Res. 28: 19-22.
- Poole AF, 1982. Brood reduction in temperate and sub-tropical ospreys. Oecologia 53: 111 – 119.
- Pucek Z. 1984. Key to the Identification of Polish Mammals. Warsaw. Poland: PWN (In Polish).
- Real J. Manosa S. Codina J. 1998. Post-nestling dependency period in the Bonelli's eagle *Hieraaetus fasciatus*. Orn. Fenn. 75: 129 – 137
- Roulin A, 2001. Food supply differentially affects sibling negotiations and competitions in barn owls *Tyto alba*. Behav. Ecol. Sociobiol. 49: 514 – 519.
- Salamolard M, Butet A, Leroux A, Bretagnolle V, 2000. Responses of an avian predator to cycles in prey density at a temperate latitude. Ecology 81: 2 428 - 2 441.
- Simmons R_7 1988. Offspring quality and the evolution of cainism. Ibis 130: 339 357.
- Simmons R. 1991. The efficiency and evolution of aerial food passing in harriers. Gabar 6: 51-56.
- Simmons R. 1997. Why don't all siblicidal eagles lay insurance eggs? The egg quality hypothesis. Behavioral Ecology 8: 544-550.
- Sokal RR, Rohlf FJ, 1981. Biometry. 2nd edn. San Francisco, USA: Freeman.
- Spaar R, 1996. Flight behaviour of migrating raptors in southern Israel. PhD Thesis. University of Basel. Sempach, Switzerland: Verlag Schweizerische Vogelwarte.
- Spellerberg IF, 1971. Breeding behaviour of the McCormick skua Catharacta maccormicki in Arctica. Ardea 59: 189 230.
- Steidl RJ, Griffin CR, 1991. Growth and brood reduction of Mid-Atlantic coast Osprey. Auk 108: 363 370.
- Strickland D. 1991. Juvenile dispersal in gray jays: dominant brood member expels sibling from natal territory. Can. J. Zool. 69: 2 935 2 945.
- Village A, 1990. The Kestrel. London: T. & A. D. Poyser.
- Vinuela J, 1999. Sibling aggression, hatching asynchrony, and nestling mortality in the black kite *Milvus migrans*. Behav. Ecol. Sociobiol. 45: 33 – 45.