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Postnatal development of Steller's Sea Eagles sexing and aging techniques

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Abstract. To evaluate the impact of varying feeding conditions on reproductive success of Steller's Sea Eagle *Haliaeetus pelagicus*, I studied development of 71 eaglets during seven breeding seasons. Significant differences between the sexes in body development are manifested at 45-50 days. According to discriminant analysis of a complex of eaglet morphometric characteristics, females comprised 45.07% of the nestlings studied. Rate of development and the number of eaglets produced were significantly correlated with hatching date. Eaglets hatched out early grew significantly slower than those hatched later. The number of eaglets per brood (soon after hatch), correlated negatively with the time of egg laying. Females hatched significantly earlier than males in nests with two eaglets of different sexes. Older siblings were usually dominant over younger ones during the first month after hatching due to difference in size. The rate of growth of younger siblings decreased significantly ($P = 0.05$) in comparison with older siblings in conditions of low food supply. Worsening feeding conditions are probably caused by changes in the hydrologic regime of water bodies upon which eagles nest, and explains the relation between water regime and growth rate of eaglets. Growth rate decreases when water level fluctuates far enough from an average optimal value. Declines in food supply related to water level may aggravate age-related differences in size, promote fratricide and lead to decreased breeding success. In years with average water level breeding success was significantly higher.

INTRODUCTION

The nesting period is the most important phase of a bird's annual cycle. It is during this period that the annual reproductive potential of the population is realized. Many traits of nesting biology of birds are aimed at promoting the better survival of the offspring. However, growth and development of the chicks also depends upon environmental conditions, and the effect of ecological factors upon natal survival may be equal to that of physiological ones (O'Connor 1977). Awareness of the principles of nestling development and their ecological and physiological requirements allow factors affecting the number, dynamics and sex and age structure of the population to be defined. The present study aimed at investigating the fundamental principles of development of nestling Steller's Sea Eagle *Haliaeetus pelagicus*

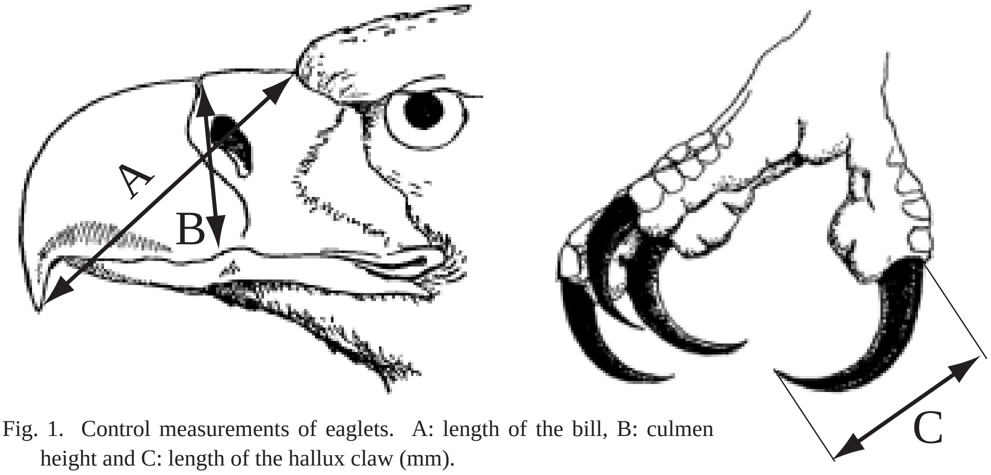

Fig. 1. Control measurements of eaglets. A: length of the bill, B: culmen height and C: length of the hallux claw (mm).

under various ecological conditions and to identify factors that affect reproductive success. An attempt to develop sexing and aging procedures based on body measurements was made.

METHODS

Data were collected at nests of Steller's Sea Eagle located on the lakes of the Lower Amur and bays along the north-eastern coast of Sakhalin during seven field seasons (1986 and 1989-1994). Development of 71 eaglets from hatching to fledging was observed. Eaglets were weighed and measured every 4-7 days. Measurements taken included: body weight (g), wing chord (mm), length of 7th primary (counting from the innermost, mm), length of 1st secondary (mm), length of the bill from its tip to the plumage edge on the front (culmen plus cere mm), culmen height (Fig. 1) length of hallux (mm), and length of tarsus (mm). Weight and linear increment was calculated as the difference between two successive measurements divided by the number of days. Fundamental indices of growth and development of eaglets were defined on the basis of study results and data from hand-reared Steller's Sea Eagles (Bogdanovich *et al.* 1994, Tcheredov 1995).

A control sample of 12 individuals (6 males and 6 females, sex defined by chromosome analysis) older than 70 days was used to investigate relations between morphometric characteristics and sex. Sex of birds, as determined in the control sample was used as a grouping variable for discriminant analysis. Results suggested an equation for sex determination based on morphometric characteristics in birds older than 70 days. This equation was used to determine sex of birds older than 70 days from a control sample (N = 71), whose development was watched from the age of month to fledging. Obtained data allowed to estimate analogous discriminant equations for the age of 50 to 70 days.

Eaglet diets (amount, size and species of prey) were studied by analyzing food remnants (cranial bones) collected on and under nests in the course of regular nest inspections. "Reverse calculation" (Vronskiy 1960) allowed specific weight and dimensional composition of prey to be evaluated. Relation of cranial bones size to body mass and linear dimensions was estimated by measuring individuals in control samples of 50 specimens for each of the frequently caught species: Crucian Carp *Carassius auratus gibelio*, Amur Catfish *Parasilurus asotus*, *Pseudobargus fulvidraco*, and Amur Pike *Esox reicherti dybowski*. Analysis was performed on 1678 prey remains, collected at 63 eagle nests in 1986, 1989, 1990, 1992 and 1994.

Factors considered critical to eaglet growth rate were: water level, hatching date (and therefore time of clutch initiation), the numbers of eaglets in the nest, and their sex and age. MANOVA and covariance analysis were used to reveal relationships between parameters. Eaglet age influenced the rate and pattern of development. Statistical estimates were made using SYSTAT 5.0.

Data on water level in the Amur River were provided by the hydrometeorological station located in Bogorodskoye village, Ulchskiy district. Shallow areas of the control water body (Lake Udyl), where Steller's Sea Eagles hunted, almost dried out when the water level in the Amur River dropped to 0-30 cm.

Nesting success was calculated as the number of fledglings per territorial pair (birds which kept to the nest area at least up to the middle of the nesting period and actively built, refurbished, and visited their nest). This was an index of reproductive potential. The causes of egg and hatchings mortality were usually unknown. The second index of reproductive success was the average number of eaglets per successfully nesting pair. This index characterizes the efficiency of the birds' reproduction in the region.

RESULTS AND DISCUSSION

Eagle's growth, sexing and aging technique

MANOVA of a control sample of 12 individuals revealed significant differences between sexes in selected morphometric measurements ($P = 0.0001$). Accurate sexing based on morphometric characteristics at an age earlier than 6-7 weeks is impossible. After 6-7 weeks differences in weight and dimensional characteristics associated with sex become significant. Linear discriminant analysis yielded the following functions for sexing eaglets in different age classes:

50-70 days of age: $Y = -0.024 \times (\text{wing length}) + 1.993 \times (\text{bill height}) + 0.366 \times (\text{bill length}) - 0.011 \times (\text{tarsus length}) - 87.202$; $P = 0.058$

70-100 days of age: $Y = 0.013\ (\text{wing length}) + 0.305 \times (\text{bill height}) + 0.182 \times (\text{bill length}) + 0.073 \times (\text{tarsus length}) - 0.065 \times (\text{claw length}) - 38.948$; $P = 0.005$

If Y is positive, an individual is a female, when negative, a male.

Using these equations, females were 45.07% of the studied population and males 54.93% ($N = 71$). This does not differ significantly from 1:1 ($P = 0.41$, $\chi^2 = 0.69$). Sex ratio

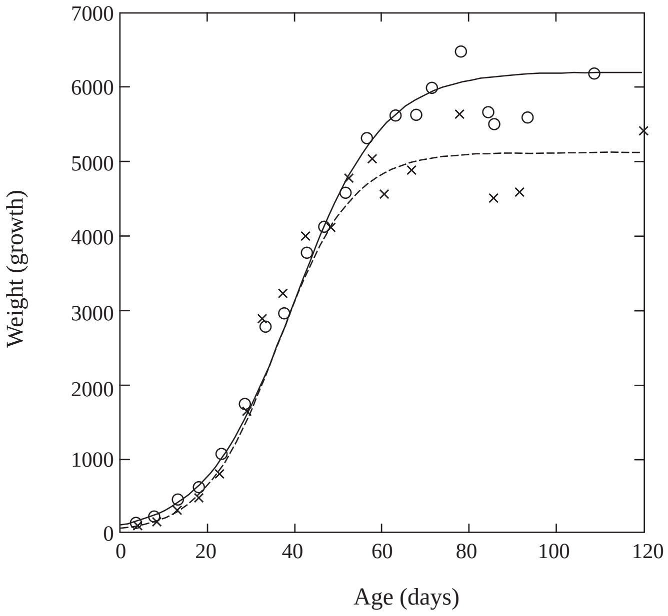

Fig. 2. Curve of the eaglet's growth. —○— : female, - - × - - : male.

approximating 1:1 is known for Bald Eagles *H. leucocephalus* (Bortolotti 1984).

Changes in body weight of growing eaglets over the whole nestling period were not constant. Weight plotted against age yeilded a sigmoidal growth curve (Fig. 2), and were described by the logistic equations (Mina & Klevezal 1976):

females: $Y = 6195 / (1 + 49.21 \times e^{-0.098 \times x})$
males: $Y = 5117 / (1 + 71.75 \times e^{-0.118 \times x})$

where Y = body weight (g) and X = age (days).

Development rates of males and females were almost equal during the first 7 weeks after hatching (Fig. 3). From age > 50-days, the rate of growth declined. This was more pronounced in males and resulted in further divergence of sexes both in weight and dimensional characteristics. Weight gain curves can be described by the equations:

females: $Y = X / (0.868 - 0.0227 \times X + 0.00032 \times X^2)$
males: $Y = X / (1.152 - 0.0358 \times X + 0.00047 \times X^2)$

where Y = rate of weight gain (g/day) and X = age (days).

Three stages of plumage development during the nestling period can be seen. Hatchlings are covered with embryonic down of silver-white color. The down is silky and glossy due to hair-like tips of the barbules. Embryonic down is replaced by brownish-gray juvenile down at the age of 16-18 days. The latter is much thicker and longer with improved insulating properties. Growth of juvenile contour feathers begins at 31 days post-hatching. It coincides

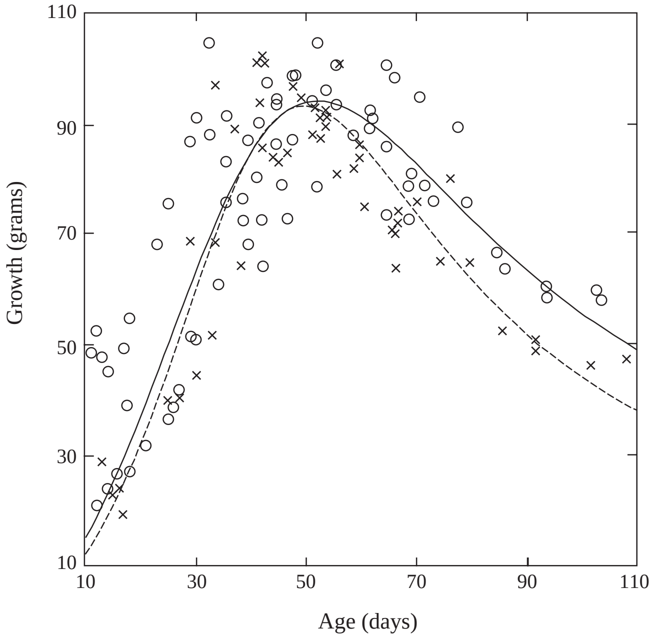

Fig. 3. Biomass increment curves for Steller's Sea Eagle. —○— : female, --×-- : male.

Table 1. Coefficients of growth for Steller's Sea Eagle body elements.

	bill length (mm)		bill height (mm)		tarsus length (mm)	
	a	b	a	b	a	b
females	13.957	0.416	8.001	0.368	34.761	0.279
males	22.783	0.280	12.845	0.245	47.371	0.200

with the appearance of sheathed stumps of the primary flight feathers. From that time onward, the growth of the primaries is virtually linear up to 90-95 day age when the 7th primary reaches its final length, averaging 400 mm in males and 450 mm in females. Growth rates of primaries do not reliably differ between sexes ($P = 0.56$) and are described by the equations:

	primaries	secondaries
females:	$Y = -194.479 + 6.501 \times X$	$Y = -126.561 + 4.875 \times X$
males:	$Y = -187.489 + 6.365 \times X$	$Y = -118.487 + 4.776 \times X$

where Y is feather length (mm) and X is age (days).

Growth rate of bill and legs is greatest in the first 2-3 weeks, after which the rate declines gradually throughout the nestling period. Growth curves of body elements can be calculated as follows:

$Y = a \times X^b$, where Y = the length of the body element (mm), and X = age (days), and where a and b are variable for each element and are described in Table 1.

Significant differences between the sexes in body development are manifested in 45-50 days, caused by a higher rate of development in males. The rate of bone growth declines after 7-8 week. The rate at which male growth slows is greater than that in females ($P < 0.001$).

The method of aging nestling eagles is based on knowledge of growth processes. In the first month (before primaries appear), eaglets can be aged using the rate of development of the body elements. Bone tissue grows particularly fast during this period (bills and legs reach 65-70% of their final length in the first month), and culmen plus cere length can be used to determine age ($P = 0.005$). In the period between hatching and 32-34 days, eaglets can be aged according to the equations

general : $Y = 0.0412 \times X^{1.614}$
females : $Y = 0.0244 \times X^{1.751}$
males : $Y = 0.1810 \times X^{1.235}$

where Y = age (days) and X = culmen length (mm)

Age of older eaglets (> 31 days) can be determined by the rate of development of the 7th primaries ($P = 0.002$ for the difference of regression coefficient from 0):

general: $Y = 31.239 + 0.145 \times X$
females: $Y = 31.917 + 0.141 \times X$
males: $Y = 30.610 + 0.149 \times X$

where Y = age (days) and X = length of the 7th primary (mm).

Shilov (1965), Ricklefs (1968), and Andreev (1990) have shown that the capacity for autonomous thermoregulation by nestlings is extremely low in the period between hatching and the time when they have attained 15-20% of their final body weight (i.e. 15-20 days for the Steller's Ssea Eagles). During this period nestlings are dependent upon adult care. Juvenile Bald Eagles are able to thermoregulate at an age of approximately 2 weeks (Bortolotti 1984). Autonomous thermoregulation by Steller's Sea Eagle nestlings also coincides with the development of the juvenile down plumage (17-20 days). After that time, the nestlings need not be brooded if the weather is good. The first seven weeks is a period of accelerated growth, during which eaglets acquire 75% of their final body weight and 80-85% of final body size. Only the growth rate of the remiges and rectricies is constant during the whole nestling period.

From the age of 50 days, the growth rate of eaglets gradually slows. Males acquire adult size 7-10 days earlier than females. Body weight increases up to 60-62 days of age in males and 70 days of age in females. Body growth ceases by 55-60 days for males and 65-70 days for females. Remiges develop to their full size by 85-90 days in males and 90-95 days in females. After remiges have grown to their full length, the surface area of the wings for females approximates 6730 cm^2 ($N = 2$). Males are smaller. Female eaglets appear to leave their nest when wing loading reaches 0.95-0.99 g/cm^2 ($N = 2$), but this is likely to vary considerably. Body weight usually decreases during the last stages of the nesting period

Table 2. Effect of hatching date on eaglets growth rate.

time of hatching	daily body weight increment (g/day)	daily wing length increment (mm/day)	daily culmen length increment (mm/day).
10-15 May	65.791	5.773	1.401
16-20 May	85.313	6.949	1.617
21-25 May	82.189	7.172	1.69
26-30 May	81.449	7.038	1.626
31 May - 5 Jun.	90.235	7.124	1.572
P	0.002	0	0.023
P1	0	0	0.016

P : level of significance of the effect of the time of clutch on the eaglet's growth rate (according to ANOVA)

P1 : level of significance of differences between growth rates of the eaglets hatched in the period 10.05-15.05 and those hatched later.

resulting in an increase in the juveniles' power efficiency (Poznanin 1979). Behavior of the young birds changes as they grow and acquire flight capabilities. They attempt to jump up and flap their wings at the age of 45-50 days, i.e., when remiges reach 35% of their final length. However, eaglets are able to fly only 85-90 days post-hatch.

Timing of laying

Artificial incubation of Steller's Sea Eagle eggs in the Moscow Zoo ($N = 6$) showed the incubation period averages 38 days (from the onset of incubation to hatching) (Tcheredov 1995). In the wild, females begin to incubate after the first egg is laid, so the time of clutch initiation may be determined if the eaglets' age is known. Eaglets hatch in the Lower Amur Region between 11 May and 3 June. Median hatching date is around 23 May. In the Sakhalin population, most of the eaglets hatch later and the median hatching date is 28 May. Extrapolating from estimated nestling ages, the peak of egg laying is about 15 April in the Lower Amur Region. The period of egg laying extends over 23 days; the earliest laying date was registered on 3 April and the latest on 26 April. Coefficient of variation of laying date is 36.56%. Average period of egg laying did not significantly differ between Lake Udyl and the Orel-Chlya lake system located 200 km closer to the sea coast (14.60 ± 0.703, $N = 45$ and 16.00 ± 2.006, $N = 21$, respectively; $P > 0.10$). On the north-eastern coast of Sakhalin, eagles laid eggs 5-6 days later, and the peak of egg laying was 20 April. Egg laying in this part of Sakhalin differs significantly from that of the Amur population (14.8 ± 0.666, $N = 57$ and 20.4 ± 1.939, $N = 14$, respectively; $P < 0.01$). Later laying and hatching dates seem to be associated with the later onset of spring in the north of the island.

Analysis of eaglet development under various ecological conditions enabled us to evaluate the effect of some factors on reproductive success. Rate of development and the number of eaglets per occupied territory varied significantly with hatching dates. Eaglets hatched earlier (between 10 and 15 May) grew significantly slower than those hatched later (Table 2). The number of eaglets per brood (registered soon after hatch) correlated negatively

Table 3. Relation between average brood size and laying date.

time of egg laying	number of eaglets	P
3-7 Apr.	1.833	0.025
8-12 Apr.	1.857	0.007
13-17 Apr.	1.666	0.09
18-22 Apr.	1.666	0.123
23-27 Apr.	1.375	1

*significance of differences between average numbers of eaglets in broods from clutches laid in 4 periods from clutches laid between 23 Apr. and 27 Apr. (Mann-Uitney test)

with the time of egg laying (coefficient of rank correlation $r = 0.23$, $P = 0.01$, $N = 117$; Table 3). Fifty-eight nests (49.6%) contained one eaglet, 57 (48.7%) two eaglets, and three eaglets were found in 2 nests (1.7%).

Comparison of growth of siblings revealed no significant relations between growth rate and age ($P = 0.405$, $N = 11$), although growth curves for older eaglets were steeper during the first 3-4 weeks. Older Bald Eagle nestlings in multiple-young nests grow, on average, 6% faster than younger ones (Bortolotti 1988). Covariance analysis of the growth rate of single Steller's Sea Eagle nestlings and the younger siblings in broods of two has shown near significant differences ($P = 0.05$, $N = 12$). No such differences have been revealed for the older sibling in these broods ($P = 0.12$, $N = 12$). This difference may result from the inhibition of growth of the younger nestling in broods of two. Growth rate of eaglets did not significantly differ in broods with one and two juveniles from the age of five weeks ($P = 0.71$, $N = 12$).

Sex ratio and timing within the hatching period

Time of egg laying was related to sex of hatchlings ($P = 0.01$). Sex ratio was 1:1 in the first five days. More females (58.9%) hatched in the middle of hatching period (the 2nd and 3rd five-day periods). In the 4th and 5th five-day periods, 77.8% of hatchlings were males. Females hatched significantly earlier than males in nests with two eaglets of different sexes ($F = 5.11$, $P = 0.03$, $N = 24$). The same is true for Bald Eagles (Bortolotti 1984, 1986). According to Bortolotti (1986), fratricide was observed more often in broods where males hatched earlier than females. In those cases, newly hatched males were larger than females, more aggressive and grew faster. The earlier hatching of females is assumed to be the result of selection aimed at survival of the maximal number of juveniles (Stalmaster 1987). Fratricide is most likely to occur in the first two weeks when differences in sizes associated with the hatching time are most evident and agonistic behavior is most pronounced. By the age of one month, conflicts between eaglets become less frequent. The rate of fratricide among sea eagles is still under question. Competition resulted in the death of only one eaglet out of 16 Bald Eagle chicks observed in seven nests (Maestrelli & Wiemeyer 1975). We have examined 19 Steller's Sea Eagles' nests with young in 1st down plumage. In only one case, a brood of three eaglets, did the youngest died of fratricide.

Food requirements

Food requirements of eaglets are closely associated with growth rate and the energy required to synthesize new tissues. Total energy used by a growing eaglet can be divided into

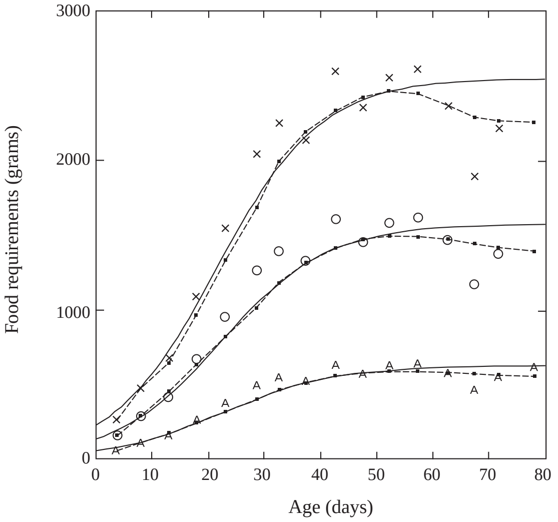

Fig. 4. Food requirements of broods with different number of nestlings. A: brood with one nestling; O: brood with two nestlings; X: brood with three nestlings. Solid line: fitted curve by the logistic equations, Broken line: smoothed graph.

that required for growth and feather synthesis, and that needed for maintenance (EM). General required energy (GE) can be calculated as follows:

GE = ((weight increment of the brood × caloric content of raw biomass) + (EM of an eaglet × number of eaglets)) / 0.7,

where 0.7 is a coefficient of utilization of food by juveniles (Dolnik 1971); caloric content of raw biomass of the eaglets is 6.70 kJ/g (Dolnik *et al.* 1982).

Energy of maintenance can be calculated according to the equation (Kendeigh *et al.* 1977):

$EM(30) = 4.472 \times m^{0.6637}$
$EM(0) = 17.342 \times m^{0.5444}$
$EM(Ta) = EM(30) + (30 - Ta) \times (EM(0) - EM(30)) / 30$,

where m = body mass (g); Ta = ambient temperature (˚C); EM(30) = energy of maintenance under thermoneutral conditions, where EM(0) = energy of maintenance under 0˚C; EM(Ta) = energy of maintenance under Ta˚C; (EM(30) - EM(0)) / 30 is heat conductance (kJ/˚C/day).

Food requirements (FI) of the growing eaglets are:

$FI = GE / (CD \times FE)$,

where CD = specific caloric value of raw matter (average CD of different species of fish

Table 4. Nestling eagle growth rates in relation to water levels in hunting areas.

	water level (cm)	daily weight increment (g/day)	daily wing length increment (mm/day)	daily culmen length increment (mm/day)
(1)	0-100	78.122	6.829	1.426
(2)	101-160	91.655	7.715	1.409
(3)	161-200	90.105	7.162	1.486
(4)	201-250	77.023	6.256	1.399
	P	0.000	0.000	0.208
	P1	0.000	0.000	0.599
	P2	0.055	0.026	0.061

P : index of significance of the effect of water level on eagles' growth rates (according to ANOVA).
P1 : index of significance of differences in growth rates related to water levels (1) and (2).
P2 : index of significance of differences in growth rates related to water levels (3) and (4).

= 5.39 kJ/g (Peredelnik *et al.* 1972)) and FE = the share of edible fish biomass = 78.7% (Stalmaster & Gessaman 1984).

Food requirements of broods with one, two and three eaglets are presented in Fig. 4 and are described by the logistic equations:

requirements of broods with 1 eaglet: $Y = 628 / (1 + 9.54 \times e^{-0.0998 \times X})$
requirements of broods with 2 eaglets: $Y = 1573 / (1 + 10.39 \times e^{-0.105 \times X})$
requirements of broods with 3 eaglets: $Y = 2546 / (1 + 10.13 \times e^{-0.108 \times X})$,

where Y = food requirements (g) and X = age (days).

The amount of fish brought by parents to the nest during a 24-hour period may be used as an indirect index of food consumption by eaglets. Food remains collected in and under nests were analyzed. Eagles brought an average of 817.01 ± 132.4 g of fish per day to nests with a single eaglet ($N = 29$) and 1545.85 ± 207.2 g to nests with two nestlings ($N = 32$), and these values were significantly different ($P < 0.001$). Over the whole nest period, average food requirements calculated from the above equation are estimated at 587.45 ± 6.85 and 1481.69 ± 16.11 g of fish per day for broods of one and two eaglets, respectively. The values for food brought to the nest are similar to the values of food required by eaglets in one and two nestling broods ($P = 0.05$ and $P > 0.05$, respectively).

Affect of water level to the growth of nestling and breeding success

Fluctuations in water level within the hunting areas of adults also affected juvenile growth rate. Such fluctuations are common in the Amur flood plain in spring and summer, resulting in differences between the lowest and highest water levels that may exceed 1.5-2 m. Shoaling of the water bodies caused by lower water levels was shown to result in a decline in the average weight of the eagle prey ($r = 0.59$, $P < 0.005$, $N = 18$; Masterov 1992). At the other end of the spectrum, fish became less accessible when water levels rose above a certain level. Both low and high water levels may cause energetic debt in growing eaglets, which, in

Table 5. Nesting success of the Steller's Sea Eagles on Lake Udyl

average number of eaglets per breeding pair			average number of eaglets per territorial pair		
year	number of nests	nesting success	number of nests	nesting success	water level*
1986	10	1.500 ± 0.167	14	1.250 ± 0.218	80.82
1989	11	1.545 ± 0.157	20	1.063 ± 0.213	17.85
1990	19	1.579 ± 0.116	30	1.200 ± 0.163	72.77
1991	5	1.400 ± 0.245	24	0.429 ± 0.202	205.00
1992	9	1.667 ± 0.167	15	1.250 ± 0.250	154.58
1993	4	1.500 ± 0.289	11	0.667 ± 0.289	9.42
1994	14	1.417 ± 0.149	21	1.063 ± 0.193	187.71

*average water level (mm) in the period of most intensive eaglet growth : 15 May - 30 June

Table 6. Percentage of different brood sizes in relation to water level*.

Number of eaglets	Water level (mm)			Total number of nests
	0-80	80-160	160-240	
0	40.0 (10)	22.4 (11)	52.8 (19)	40
1	28.0 (7)	32.7 (16)	27.8 (10)	33
2	32.0 (8)	44.9 (22)	19.4 (7)	37

*number of nests (broods) is given in brackets

turn, affects their growth rates (Table 4). Increments in body weight and linear dimensions of wing and bill during the nest period were significantly lower in both extremely low and extremely high water conditions (except culmen increment in low water conditions). In Bald Eagles prey delivery rates was related to juvenile growth rate (Bortolotti 1988).

Estimated nesting success of eagles on the lakes of the Lower Amur region during 7 years averaged 0.986 ± 0.179 fledglings per territorial pair ($N = 135$) and 1.514 ± 0.126 fledglings per nesting pair ($N = 72$). Nesting success by years is presented in Table 5. Nesting success depends, to certain extent, upon fluctuations of the water level within the hunting areas. A chi-square test of a contingency table (“number of eaglets in the nest” vs. “water level in the first 6-7 weeks after hatch”) was significant ($P = 0.05$; Table 6). Nesting success was significantly greater in years with water levels close to long-term averages. Nesting success tended to decline and the number of empty nests increase in years when the water level was extremely high (Mann-Whitney test, $P = 0.002$, $N = 70$). Low water levels also caused an increase in the proportion of abandoned nests ($P = 0.15$, $N = 73$). The size of Bald Eagle clutches does not depend upon feeding conditions. Those conditions, however, significantly affect the number of surviving eaglets (Hansen 1987).

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