
RESEARCH ARTICLES

ОРИГИНАЛЬНЫЕ СТАТЬИ

**REPRODUCTION EFFICIENCY OF THE STELLER'S SEA EAGLE
ON SAKHALIN ISLAND AND THE LOWER AMUR (RUSSIA)****Vladimir B. Masterov¹, Michael S. Romanov²** ¹*Lomonosov Moscow State University, Russia**e-mail: haliaetus@yandex.ru*²*Keldysh Institute of Applied Mathematics of RAS, Russia**e-mail: romanov.eagle@gmail.com*

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Since the mid-2000s, we have been monitoring the status of two *Haliaeetus pelagicus* populations, breeding on Sakhalin Island (438 nesting territories) and the lower reaches of the River Amur (350 nesting territories), Russian Far East. The data were collected between 2004 and 2019, during 12 field seasons in each study area. The main focus was on reproductive vital rates: territory occupancy, the proportion of laying pairs, breeding success and brood size. Their combination determines how many fledglings the territory eventually produces (productivity and territory performance). Additionally, we estimated offspring loss by various causes. Finally, we recorded all *H. pelagicus* occurrences to characterise the population structure, i.e. the proportion of immatures and breeder-to-floater ratio. Our results showed that all characteristics varied greatly over time and space, and also varied across regions. The overall reproduction efficiency was quite low in both study areas: one nesting territory on the Lower Amur produces 0.51 fledglings per year, and 0.35 fledglings per year on Sakhalin Island. The mean productivity on Sakhalin Island was also lower than on the Lower Amur: 0.51 and 0.62 fledglings per occupied territory annually, respectively. This difference between study areas is mostly due to predation by *Ursus arctos*, which takes 18% of nestlings on Sakhalin but not on the Lower Amur. Apart from direct loss, *U. arctos* predation causes indirect effects on the *H. pelagicus* population by affecting territory occupancy and the proportion of laying pairs in the subsequent year. We revealed two linear temporal trends, both for the Sakhalin population (decrease in the proportion of laying pairs and increase in nestling mortality). However, more research and data analysis are needed to explain the low breeding performance in both study areas and guide conservation efforts to stabilise or recover the *H. pelagicus* populations.

Key words: brood size, brown bear, brown bear predation, *Haliaeetus pelagicus*, nesting success, population monitoring, productivity, sensitive data, territory occupancy, *Ursus arctos*

Introduction

Haliaeetus pelagicus (Pallas, 1811) (hereinafter – Steller's Sea Eagle) is a Vulnerable raptorial species whose global population is estimated at 3600–3800 individuals (BirdLife International, 2016) or 6000–7000 individuals (Masterov et al., 2018). Due to a limited breeding range (Russian Far East) and low productivity, the species is categorised in the IUCN Red List as a globally threatened (Vulnerable) taxon (BirdLife International, 2016), enlisted in the Red Data Book of the Russian Federation (Danilov-Danilyan et al., 2001), and is protected by a number of international conventions and bilateral agreements.

Despite the great conservation status of the Steller's Sea Eagle, little is known about its population state in much of the breeding range. Due to the remoteness of the Far East region, regu-

lar studies of this raptor are scarce, with only a few exceptions, related to the activity of research groups led by Eugene Potapov in the Magadan Region (e.g. Potapov et al., 2013) and Vladimir Masterov on Sakhalin Island and the Lower Amur Region (Masterov et al., 2018). However, the information is insufficient even from these parts of the species range.

At the same time, there is evidence of various hazards for this species from poisoning by heavy metals and chlorinated hydrocarbons (Iwata et al., 2000; Kurosawa, 2000; Nakagawa, 2011), depletion of food resources (Lobkov, 2002), forest fires (Burenina, 2007), climate change (Potapov et al., 2012), predation by *Ursus arctos* (Linnaeus, 1758) (hereinafter – brown bear) (Romanov & Masterov, 2020a) as well as disturbance at nest sites, direct persecution, habitat alteration and

other anthropogenic changes. There are already some warning signs of possible population decline, such as low productivity (Potapov et al., 2010, 2012) and a decrease in the proportion of immature birds in the population (Potapov et al., 2000; Masterov & Romanov, 2014), the suggestion being supported by the results of matrix population modelling (Romanov & Masterov, 2020b). Therefore, a thorough assessment of the global population is required.

Two of the largest nesting populations of this species inhabit Sakhalin Island and the lower reaches of the River Amur (Masterov et al., 2018). From 2004, we monitored the Steller's Sea Eagle populations in these regions, which allowed us to accurately estimate the primary vital rates of the Steller's Sea Eagle reproduction together with their spatial and temporal variability. The results of the monitoring were published in the Metadata dataset on Global Biodiversity Information Facility (GBIF) (Romanov & Masterov, 2021).

The main purpose of the study is the analysis of the collected data to assess the Steller's Sea Eagle reproduction efficiency in both study areas. Our objectives were: 1) assessing the breeding efficiency of both Steller's Sea Eagle populations; 2) estimating its individual components (vital rates); 3) identifying the key factors affecting the Steller's Sea Eagle reproduction.

Material and Methods

Study areas

We conducted field studies in two regions of the Russian Far East, Sakhalin Island (Sakhalin Region) and the lower reaches of the River Amur (Khabarovsk Krai). Therefore, there are two study areas on the island and the continent, named «Sakhalin» and «Lower Amur», respectively (Fig. 1).

The «Sakhalin» study area stretches from the South to the North, encompassing the coasts of Lunsky, Nabil, Nyisky, Chaivo, and Piltun bays together with the lower reaches of the rivers that flow into these bays. The northern and southern boundaries of the study area correspond to latitudes 53.4° N and 51.1° N, respectively, and the length of the area from the South to the North is approximately 250 km. The eastern boundary coincides with the coastal line, the western boundary lies at a distance of approximately 20–30 km from the coast depending on the hydrological characteristics. The area potentially suitable for sea eagles is approximately 3280 km².



Fig. 1. The Steller's Sea Eagle global range and two study areas, «Lower Amur» (Khabarovsk Krai) and «Sakhalin» (Sakhalin Region).

The «Lower Amur» study area encompasses the lower reaches of the River Amur together with the channels of the River Amur floodplain and associated large and small lakes with rivers flowing into them. The largest lakes are Udyl, Kizi, Kadi, Irkutskoe and Dudinskoe. The northern and southern boundaries of the study area are 52.7° N and 51.2° N. The western border passes along the River Pilda (139.5° E), with the eastern border bounded by the coast of the Tatar Strait. The total area is about 4000 km². Co-ordinates of the rectangle covering both study areas: latitude 51.1° E and 53.7° E, longitude 139.5° N and 143.7° N.

Study objects

Typical Steller's Sea Eagle's nests are large conspicuous structures approximately 1.5–2 m wide, made of branches and normally found in the upper part or on the top of the tree. Often Steller's Sea Eagles build several nests, among which they choose one for breeding, while others (called alternate, or alternative nests) are either used for perching, eating, and others, or go unused in a given year.

Like most raptors, Steller's Sea Eagles are territorial animals. Mated eagle pairs occupy certain areas (called nesting territories) in a suitable habitat, in which they breed. Territorial pairs can hold their nesting territories for many years. A full clutch contains 1–2 (rarely 3) eggs, but, even if the third nestling hatches, it usually does not survive, so that broods of three are exceptionally rare (see the reported exceptions in Utekhina 2004). Thus,

normally, a pair of Steller’s Sea Eagles raises 1–2 young individuals per breeding attempt. However, for some reason (after harsh wintering, under unfavourable conditions of the season, after a failed breeding attempt, and others), they may choose to skip breeding but still defend nesting territories.

Besides the Steller’s Sea Eagle, there is another large raptorial species in the study areas, the *Haliaeetus albicilla* (Linnaeus, 1758), but they are not as numerous. We included data from *H. albicilla* too, because the two species sometimes occupy nests and territories of each other.

Temporal scope

Most of the data were collected during summer, from early July to late August. During this period nestlings reach fledging age, so it is easier to assess nesting results. In some years, only on Sakhalin, we collected data during April, when Steller’s Sea Eagles begin to lay eggs.

Summer field studies on Sakhalin Island were conducted in 2004–2014, 2018–2020. Studies on the Lower Amur were conducted in 2006–2010

and 2012–2019. Spring counts on Sakhalin were conducted in 2006–2008.

Sampling

In our study, we largely follow the terminology outlined by Postupalsky (1974) and revised by Steenhof & Newton (2007) and by Steenhof et al. (2017). According to the definition, a nesting territory (sometimes referred to as territory) is an area that contains (or historically contained) one or more nests within the home range of a mated pair (Steenhof et al., 2017) (Fig. 2). That is why researchers focus on breeding territories rather than individual nests (e.g. Postupalsky, 1974; Lobkov, 1990).

Inspection of a Steller’s Sea Eagle territory implies visiting all its nests, observing their condition and tracks of bird activity, detecting a breeding attempt (if any), and making the final judgement on the territorial status. Our fieldwork focussed on working with nests and territories to estimate the territorial status and breeding outcome. Additionally, we registered all sightings of the Steller’s Sea Eagles to assess the age and territorial structure of the populations.

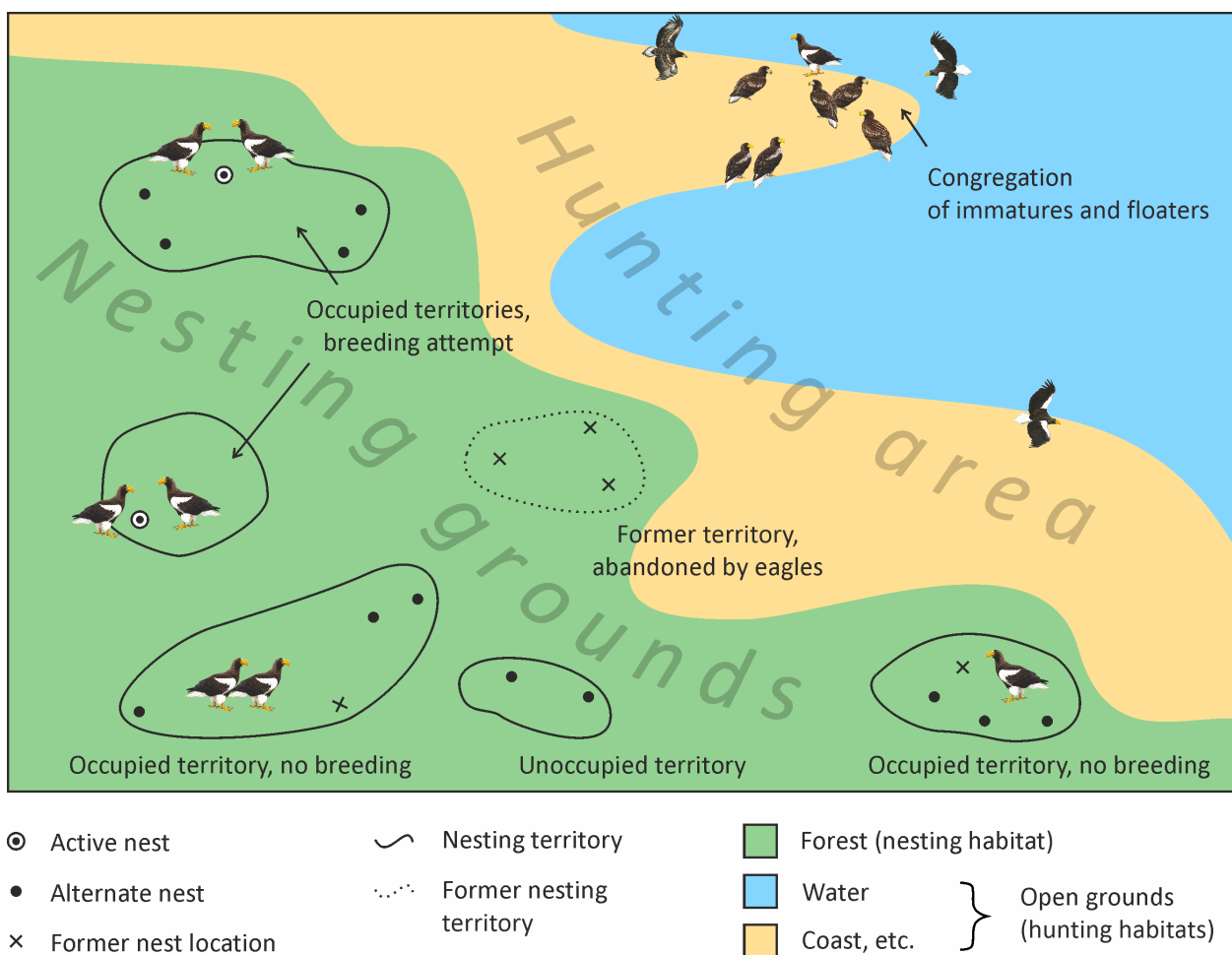


Fig. 2. The structure of the Steller’s Sea Eagle nesting territories (a scheme). There are six nesting territories shown, among which one ceased to exist. Four of the existing territories are currently active (there is active nest where the breeding is going on), and one is not active (no breeding is going on).

Nesting territories and their status

When working on nesting grounds, we inspected known Steller's Sea Eagle nests and searched for new ones. For each nest, we determined its status and, if reproduction is going on, the number of fledglings. Since one Steller's Sea Eagle pair can hold several nests, we grouped the nests into nesting territories. Nesting territories are not immutable; they have neither clear boundaries nor a constant list of nests. Sometimes nests may change their owners. Furthermore, a territory may even split in two if a new territorial pair settles in. Deciding which territory a nest belonged to, we used their proximity and occupancy status. The general criterion of nest proximity was doubled radius of the defended area around the nest (about 200 m), so generally nests situated closer than 400 m from each other were referred to the same territory. We also took into account the presence of territorial birds and their behaviour. Each year we inspected 124–283 territories on Sakhalin Island and 20–200 territories on the Lower Amur, depending on weather conditions, the volume of fieldwork and other logistical constraints.

Bird census

During the fieldwork, we performed an assessment of the age and territorial structure of the Steller's Sea Eagle populations. For this purpose, we inspected as much as possible suitable habitats of territorial Steller's Sea Eagles and areas of congregations of non-territorial birds and registered all individuals we observed. In addition to these special observations, we recorded all occasional sightings of Steller's Sea Eagles.

During 2004–2019 we made more than 7000 observations of individual Steller's Sea Eagles and their groups. We aimed to avoid repeated counts within the same year, but obviously, the same individuals could be repeatedly met in different years.

Adult, immature, and juvenile birds are well distinguished by their age-specific plumage. Also, we recorded the apparent territoriality status of adults: initially, we defined it in the field by expert judgment, based on the birds' behaviour (e.g. territorial, defensive, courtship), location relative to nesting areas, and other circumstances of the observation (habitat, number of birds, and others). Subsequently, these estimates were revised on mapped data, and the final judgment was made. In doubtful

cases, adult birds registered farther than 1.5 km from the nearest Steller's Sea Eagle nest were classified as floaters, the threshold being based on our observations and energetic constraints of the species.

Database structure

A description of the database was published as a metadata dataset in the GBIF (gbif.org) (Romanov & Masterov, 2021). Full disclosure of these data was not possible for ethical reasons, since the publication of co-ordinates and the indication of places of high population density could potentially cause additional harm to this unique Vulnerable species.

The database essentially consists of five related tables: Nests, Territories, Nest status, Territory status, and Birds. They also represent supplementary tables (Fig. 3, Table 1S, Table 2S, Table 3S, Table 4S, Table 5S, Table 6S).

Software used

A relational database was developed in MS Access (Microsoft Office 2016, v. 2111) for data entry, storage, manipulation and extraction for subsequent statistical processing and spatial analysis. Geographical data were processed in the QGIS v. 3.10 program (QGIS Development Team, 2021). All calculations were performed in R statistical software environment, v. 4.1.2 (R Core Team, 2021). The map interpolations were made in QGIS with the Inverse Distance Weighted (IDW) Interpolation Plugin. This plugin generates interpolation of a point vector layer using IDW algorithm: sample points are weighted during interpolation such that the influence of one point relative to other declines with distance from the given pixel. The interpolation radius was set to 5 km.

Data analysis

Uncertainty of the breeding outcome and its treatment

It is not always possible to correctly determine the status of a nesting territory and to count the number of young (Steenhof & Newton, 2007). Following the recommendations of Fuller et al. (1995), we observed each nest for at least 1 h unless we were sure that the entire brood had been seen. In most cases this worked well; however, in some cases we were not able to see the nest contents, especially in elevated nests, so uncertainty remained.

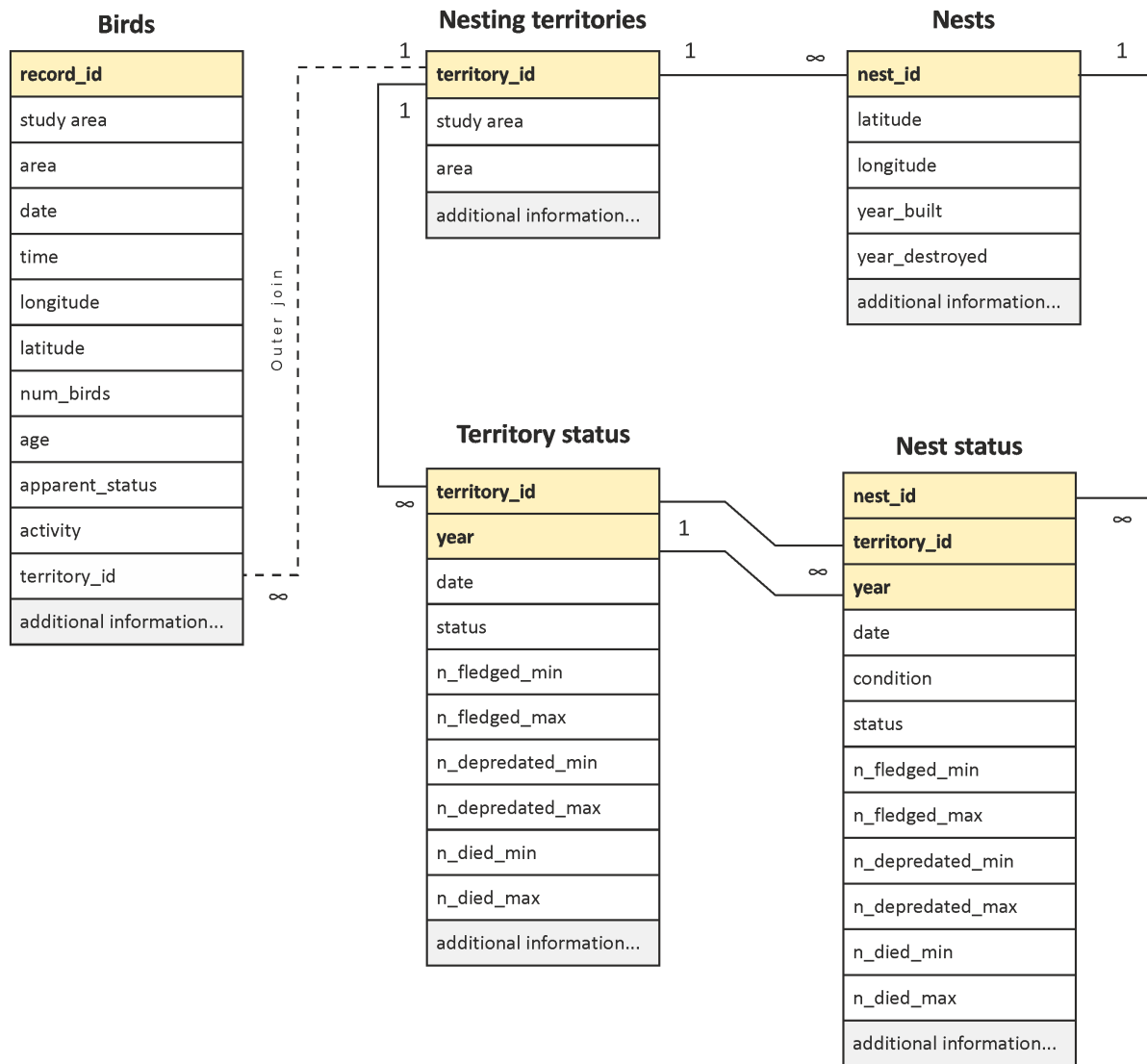


Fig. 3. Scheme of the database (main tables, main fields are shown) in Romanov & Masterov (2021).

In most cases, the uncertainty arose relatively to the number of nestlings depredated by the brown bear, since their remains were not always found (58% of depredated nests). In some cases, brown bears dragged nestlings away from the nest to eat elsewhere. In other cases, escaping nestlings can fledge prematurely. Even if they do not die or get injured during their fall from the nest, they are to be killed by terrestrial mammals on the ground afterwards. In all these cases nestling remains may not be found, so the number of killed young may be underestimated.

In the case of nestling mortality from other causes, their number may not always be ascertained (19% of suffered nests). In some cases, there are remains of one dead nestling, but the presence of another is possible.

Finally, uncertainty may emerge even in successful nests if nestlings are hardly seen because of poor observational conditions (dense foliage, fog, etc.). In some cases (12% of successful

nests) we were able to see only one nestling but could not exclude the presence of another one.

When we were unable to determine the exact number of nestlings in any category (fledged, depredated, or dead) we recorded it as an interval (1–2). Also, we estimated the expected number of nestlings with different fates. For successful nests, we assigned the expected number of fledglings the average brood size in the given year. If we did not know the number of depredated nestlings, we also assigned it the average brood size, because brown bears usually kill all nestlings in the brood. In case of uncertainty in nestling mortality, if we were not sure of the number of lost nestlings, we assigned the nest the mean number of dead nestlings from nests with known mortality.

Vital rates and their estimation

Breeding is a multistage process which aspects can be described by separate characteris-

tics (e.g. see details in Masterov et al., 2018). The main stages are: return from wintering grounds and occupation of nesting territories, egg-laying, chicks rearing and fledging. This process takes a long time, about five or six months from March to August, and the breeding can fail at each stage (Fig. 4).

Our sampling method allows us to assess the breeding efficiency of a population at each stage. We estimated eight parameters of Steller’s Sea Eagle reproduction. These include four elementary (original) vital rates, two derived parameters, and two factors of nesting failure.

Elementary (original) vital rates

We distinguish four vital rates which reflect different stages of the breeding season and independently contribute to Steller’s Sea Eagle reproduction. These are territory occupancy, breeding activity (proportion of laying pairs), nesting success, and brood size. Territory occupancy is calculated as the proportion of occupied territories among all existing territories. The latter means that, although the definition of the term (see above) includes areas which «historically contained» nests, we decided to exclude from the analysis territories which nests ceased to exist:

$$Occupancy = \frac{N_{occupied\ territories}}{N_{all\ existing\ territories}}$$

Breeding activity characterises what proportion of territorial pairs try to breed. The breed-

ing activity, or proportion of laying pairs, is calculated as the ratio of the number of laying pairs to the number of all territorial pairs, or, equally, the ratio of the number of active territories to the number of occupied territories:

$$Breeding\ activity = \frac{N_{laying\ pairs}}{N_{territorial\ pairs}} = \frac{N_{active\ territories}}{N_{occupied\ territories}}$$

Steenhof et al. (2017) declared the term «active nest» deprecated and advised against using it unless it is clearly defined. The replacement term is «egg-laying pairs». Agreeing with the authors, we still like the former term as shorter, so we use both of them as synonyms. If a breeding attempt fails in the early stages of the field season, it may go undetected, in which case the territory is misclassified as occupied but not active. This makes this vital rate biased downwards. Therefore, this parameter alone is not very reliable. However, we argue that it is useful in a broader context, together with other vital rates. A nesting attempt is considered successful if at least one young reaches the minimum acceptable age for assessing success (Steenhof & Newton, 2007), which is for the Steller’s Sea Eagle about 80 days. Nesting success is calculated as the proportion of successful breeding attempts:

$$Nesting\ success = \frac{N_{successful\ breeding\ attempts}}{N_{all\ breeding\ attempts}}$$

Brood size is the number of fledglings per successful breeding attempt, calculated based on nests with an exactly known number of fledglings:

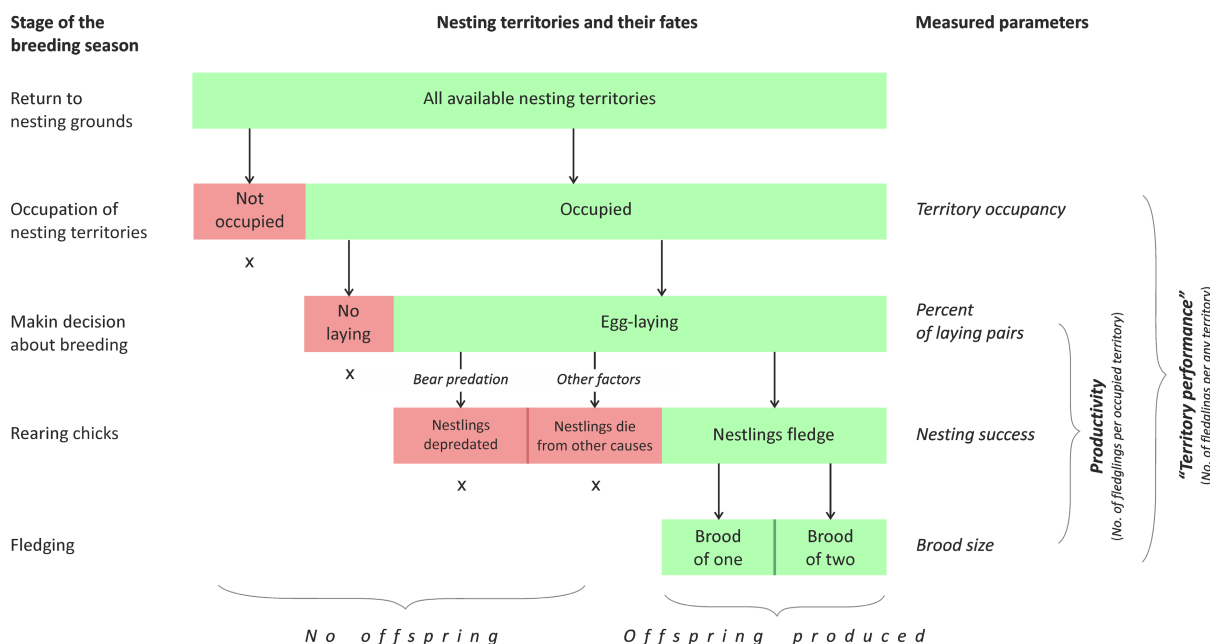


Fig. 4. Steller’s Sea Eagle reproduction vital rates, their inter-relations and corresponding stages of the breeding season.

$$\text{Brood size} = \frac{N_{\text{fledged nestlings}}}{N_{\text{successful breeding attempts}}}$$

Derived vital rates

Ultimately, what matters for a population is the total number of offspring produced. The most commonly used vital rate for assessing reproduction efficiency is productivity, which is the number of successfully fledged nestlings per territorial pair (or, the same, per occupied territory). However, in some cases, the exact number of grown nestlings remained unknown (see above the section «Uncertainty of the breeding outcome and its treatment»). Therefore, we derived this vital rate by the alternative equation:

$$\text{Productivity} = \text{Breeding activity} \times \text{Nesting success} \times \text{Brood size}$$

This characteristic is based on three of the four elementary vital rates. However, the fourth vital rate, territory occupancy, is also of great importance, so we suggest another derived characteristic, based on all four elementary vital rates, which we call here territory performance. This parameter shows how many chicks one territory produces, regardless of its status. It is calculated as a product of four elementary vital rates:

$$\text{Territory performance} = \text{Territory occupancy} \times \text{Breeding activity} \times \text{Nesting success} \times \text{Brood size}$$

Factors of nesting failure

During all the years of monitoring, we kept finding dead nestlings or their remains. One of the most common reasons for nesting failure was predation by the brown bear. Therefore we decided to estimate the predation pressure separately and distinguished it from all other factors. The brown bear predation rate (or proportion of depredated nestlings) is calculated as the proportion of depredated nestlings from all nestlings:

$$\text{Brown bear predation rate} = \frac{N_{\text{depredated nestlings}}}{N_{\text{all nestlings}}}$$

As was said above, nestling remains were not always found, and uncertainty emerges in the corresponding equation term. Ignoring it would lead to a severe underestimation of the number of depredated nestlings. However, we know that brown bears tend to take all nestlings from the brood, so for such nests, we estimated the expected number of depredated nestlings by multiplication of the number of nests suffered from predation by mean brood size in this year:

$$N_{\text{depredation nestlings}} = N_{\text{predation nests}} \times M_{\text{brood size}}$$

The nestling mortality rate (proportion of dead nestlings) quantifies nestling mortality from all other causes. It is calculated as the proportion of dead nestlings to all nestlings:

$$\text{Nestling mortality rate} = \frac{N_{\text{dead nestlings}}}{N_{\text{all nestlings}}}$$

Therefore, we estimated eight vital rates of Steller's Sea Eagle reproduction, including four elementary rates (territory occupancy, breeding activity or proportion of egg-laying pairs, nesting success, brood size), two derived characteristics (productivity and territory performance), and two factors of nesting failure (brown bear predation pressure and nestling mortality from other causes).

Results

From 2004 to 2019, we made 4188 observations of territory status, detected 2705 occupied territories and 1355 breeding attempts. On Sakhalin, 863 breeding attempts produced 828–900 (estimated number 856) fledglings. Also, 180–292 (estimated number 213) nestlings were killed by the brown bear, and 87–99 (estimated number 88) died in the nests (Table 7S). On the Lower Amur, 492 breeding attempts produced 590–678 (621) fledglings, two nestlings were killed by brown bears, and 47–59 (estimated number 49) nestlings died in the nests (Table 8S). Vital rates, calculated based on the field results, are presented in Table 1 and Fig. 5.

Exploratory data analysis showed that characteristics greatly varied between years. Two of the four elementary vital rates, breeding activity and brood size, did not significantly differ between study areas.

Another two characteristics, territory occupancy (0.69 vs. 0.82) and nesting success (0.74 vs. 0.94, respectively), were lower on Sakhalin than in the Lower Amur. This led to a 20% difference in productivity on Sakhalin vs. Lower Amur (0.51 and 0.61 fledglings per occupied territory, respectively) and an even greater (nearly 30%) difference in territory performance: one Sakhalin territory produces 0.35 fledglings per year, whereas one Lower Amur territory grows 0.51 fledglings per year.

The main reason for the low nesting success of Steller's Sea Eagles on Sakhalin was intensive brown bear predation (see Electronic Supplement 2). A total of 18% of nestlings (from 5% to 43% in various years) were killed by brown bears. On the contrary, on the Lower Amur cases of the brown bear predation were exceptionally rare: only two registered cases, both in 2006,

which means 0.3% of all nestlings. Nestling mortality from other causes was similar between regions 7–8%. The proportion of immatures was

somewhat higher on Sakhalin vs. Lower Amur (0.17 vs. 0.14, respectively), and so was the proportion of floaters (0.29 vs. 0.21).

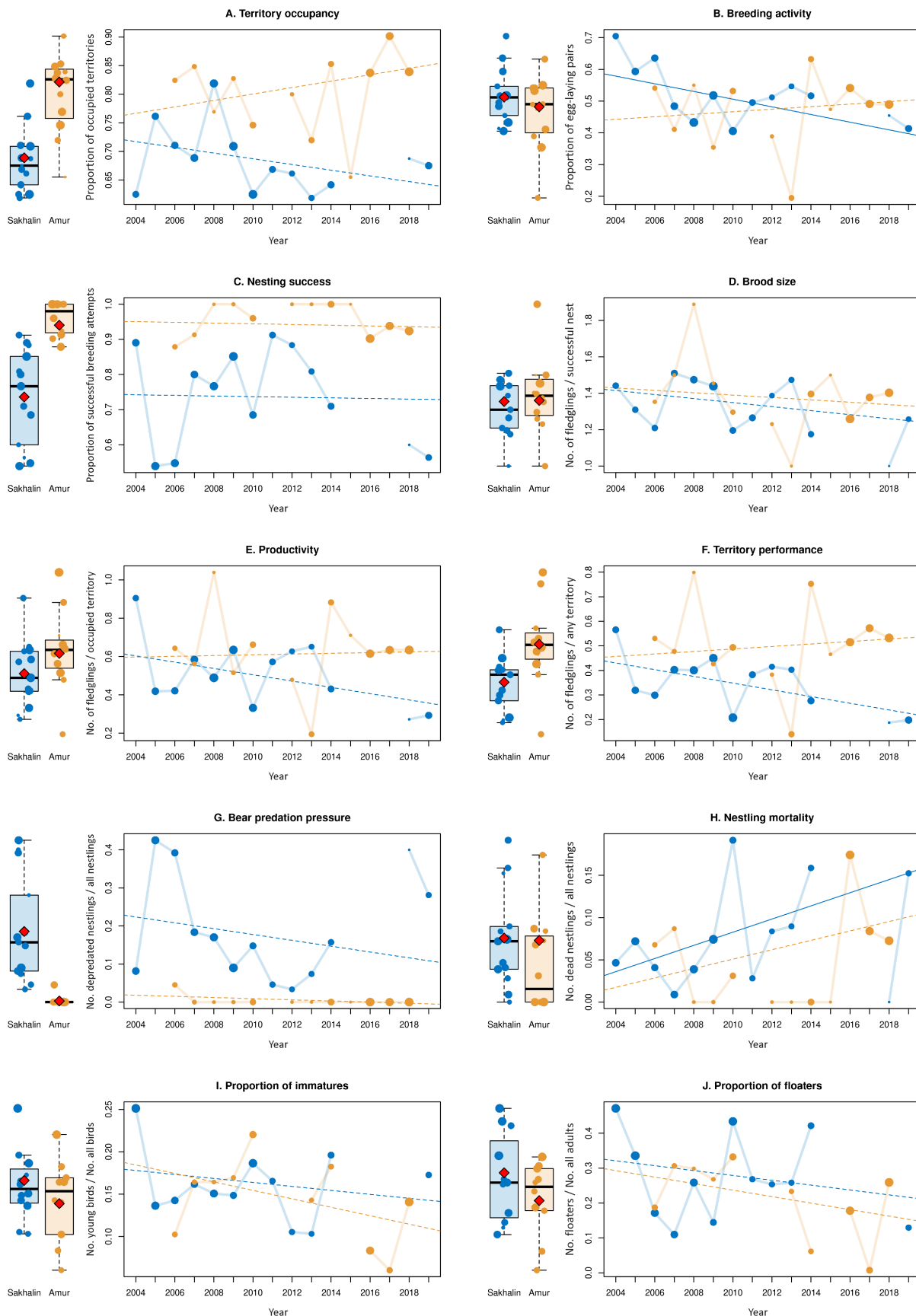


Fig. 5. Steller's Sea Eagle vital rates and their temporal dynamics. Solid lines depict significant trends (linear regression, $p < 0.05$), dashed lines are possible trends.

Table 1. Annual dynamics of vital rates of the Steller's Sea Eagle reproduction (yearly means and weighted means for all years of monitoring)

Year	Territory occupancy	Breeding activity	Nesting success	Brood size	Productivity	Territory performance	Brown bear predation	Nesting mortality	Percent of immatures	Percent of floaters
Sakhalin study area										
2004	0.63	0.70	0.89	1.44	0.90	0.57	0.08	0.05	0.25	0.47
2005	0.76	0.59	0.54	1.31	0.42	0.32	0.43	0.07	0.14	0.34
2006	0.71	0.64	0.55	1.21	0.42	0.30	0.39	0.04	0.14	0.17
2007	0.69	0.48	0.80	1.51	0.58	0.40	0.18	0.01	0.16	0.11
2008	0.82	0.43	0.77	1.47	0.49	0.40	0.17	0.04	0.15	0.26
2009	0.71	0.52	0.85	1.44	0.63	0.45	0.09	0.07	0.15	0.14
2010	0.63	0.41	0.68	1.20	0.33	0.21	0.15	0.19	0.19	0.43
2011	0.67	0.50	0.91	1.27	0.57	0.38	0.05	0.03	0.17	0.27
2012	0.66	0.51	0.88	1.39	0.63	0.42	0.03	0.08	0.11	0.25
2013	0.62	0.55	0.81	1.47	0.65	0.40	0.07	0.09	0.10	0.26
2014	0.64	0.52	0.71	1.18	0.43	0.28	0.16	0.16	0.20	0.42
2018	0.69	0.45	0.60	1.00	0.27	0.19	0.40	0.00	–	–
2019	0.68	0.41	0.56	1.26	0.29	0.20	0.28	0.15	0.17	0.13
All years	0.69	0.51	0.74	1.35	0.51	0.35	0.18	0.08	0.17	0.29
Lower Amur study area										
2006	0.82	0.54	0.88	1.35	0.64	0.53	0.05	0.07	0.10	0.19
2007	0.85	0.41	0.91	1.50	0.56	0.48	0.00	0.09	0.16	0.31
2008	0.77	0.55	1.00	1.89	1.04	0.80	0.00	0.00	0.16	0.30
2009	0.83	0.35	1.00	1.45	0.52	0.43	0.00	0.00	0.17	0.27
2010	0.75	0.53	0.96	1.30	0.66	0.49	0.00	0.03	0.22	0.33
2012	0.80	0.39	1.00	1.23	0.48	0.38	0.00	0.00	–	–
2013	0.72	0.19	1.00	1.00	0.19	0.14	0.00	0.00	0.14	0.23
2014	0.85	0.63	1.00	1.40	0.88	0.75	0.00	0.00	0.18	0.06
2015	0.66	0.47	1.00	1.50	0.71	0.47	0.00	0.00	–	–
2016	0.84	0.54	0.90	1.26	0.61	0.51	0.00	0.17	0.08	0.18
2017	0.90	0.49	0.94	1.38	0.63	0.57	0.00	0.08	0.06	0.01
2018	0.84	0.49	0.92	1.40	0.63	0.53	0.00	0.07	0.14	0.26
All years	0.82	0.48	0.94	1.36	0.62	0.51	0.003	0.07	0.14	0.21

There were only two significant trends over time, both on Sakhalin: a decrease in breeding activity (linear regression, $p < 0.05$) and an increase of nestling mortality (linear regression, $p < 0.05$). However, there were some possible trends, which require testing by more robust statistical analysis: decreases in territory occupancy, productivity and territory performance on Sakhalin (Fig. 4A,E,F), an increase of nestling

mortality on the Lower Amur (Fig. 4H), and a decrease in the proportion of immatures and proportion of floaters in both study areas (Fig. 4I,J).

Mapping of the spatial distribution of vital rates reveals their patchy nature. Both nesting failure factors, brown bear predation and nestling mortality have a clustered structure, which in turn leads to the patchy distribution of territory performance (Fig. 6).

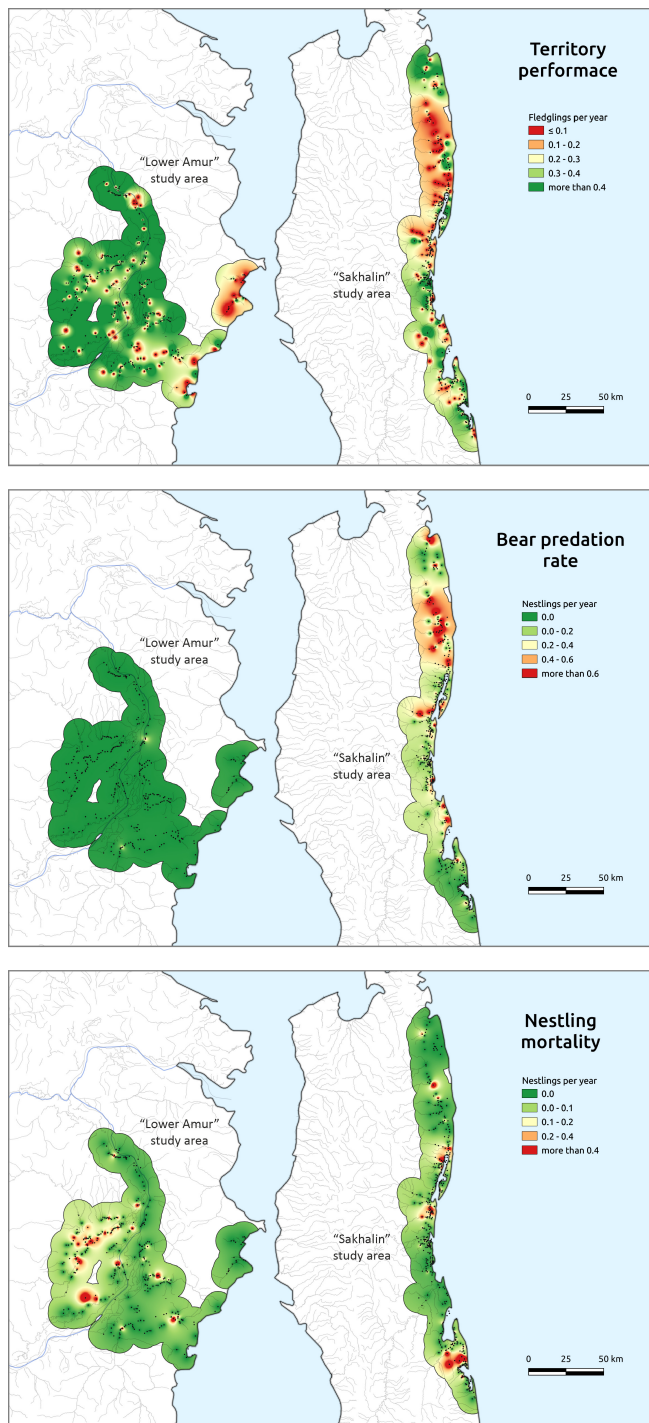


Fig. 6. Spatial distribution of some vital rates of the Steller’s Sea Eagle: territory performance (number of fledglings produced by the territory per year), rate of brown bear predation, nestling mortality.

Discussion

Our preliminary analysis of the Steller’s Sea Eagle vital rates on Sakhalin Island and the Lower Amur reveals several negative factors, which raises concern for the populations’ sustainability. First is the high predation rate of the brown bear, which take 18% of Steller’s Sea Eagle offspring on Sakhalin Island. As we showed before, this factor, in addition to the immediate damage to the population, causes an indirect effect on Steller’s Sea Eagle pairs through negative breeding experience and destruction of their nest structures (Romanov & Masterov, 2020a). As was reported earlier on the material of 624 breeding attempts, nesting failure is followed by a decrease in several vital rates (ibid.). As a result, the next year after nestling mortality or brown bear predation, a territory produces twice less offspring (0.26 and 0.32 fledglings) than after a successful nesting (0.60 fledglings) (Table 2). Therefore, a lower territory occupancy on Sakhalin Island can be explained by the consequences of brown bear predation. Besides, the observed decline in breeding activity and a possible decline in territory occupancy on Sakhalin Island can be also related to the brown bear predation.

Mortality from other causes leads to the loss of 7–8% of offspring. Possible causes of nestling mortality are climate and weather conditions, disturbance on nest sites and (only on the continent) water levels of the River Amur (Masterov et al., 2018). Among the other factors influencing the productivity of Steller’s Sea Eagles, habitat quality is worth mentioning (Fig. 7).

Although the reproductive efficiency of the Amur Steller’s Sea Eagles is 20% higher than that of Sakhalin ones, it is still far from optimal. For example, in the late 1990s the productivity of the Sakhalin population was 0.79 fledglings per occupied territory (Masterov et al., 2000), and in the late 1980s – early 1990s even higher, 0.8–1.4 fledglings per occupied territory (Masterov, 1995). Our matrix modelling (Romanov & Masterov, 2020b) showed that such productivity is not sufficient for population maintenance, and predicts a decline in both Steller’s Sea Eagle populations.

Table 2. Indirect influence of the Steller’s Sea Eagle nesting success on the subsequent reproduction (Sakhalin Island, according to Romanov & Masterov, 2020a)

Vital rates in the next year	Nesting results in the initial year		
	Success	Nestling mortality	Brown bear predation
Territory occupancy	0.89	0.84	0.72
Proportion of egg-laying pairs	0.62	0.53	0.51
Nesting success	0.78	0.53	0.57
Brood size	1.40	1.22	1.50
Territory performance	0.60	0.26	0.32

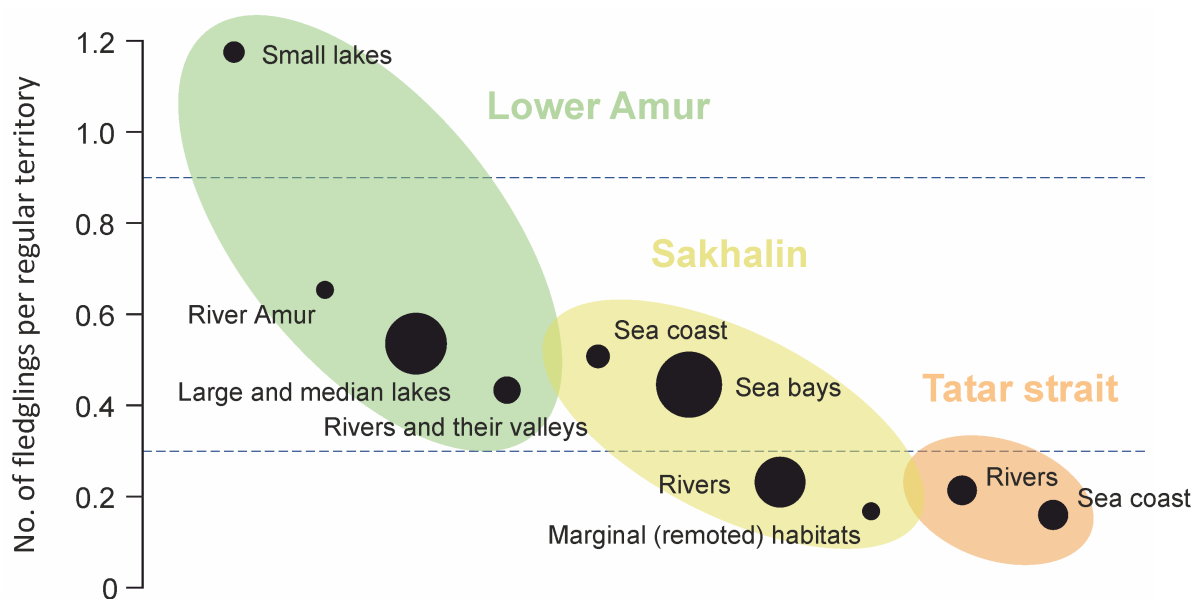


Fig. 7. Territory performance of Steller's Sea Eagles in main habitats on the Lower Amur, Sakhalin Island, and the coast of Tatar Strait. Circle area is proportional to the sample size, the dashed lines separate significantly different habitat groups (according to Masterov et al., 2018).

This suggestion is supported by negative, though insignificant, trends in population structure: proportion of immatures and proportion of floaters, in both study areas. The low proportion of immatures in a Steller's Sea Eagle population may indicate population decline, though this characteristic is not unambiguous and should be interpreted with care (Stalmaster, 1987). Floaters (non-territorial adults) play a buffer role in a raptor population and, in general, the larger the reserve of floaters the more stable the breeding segment (Hunt, 1998). On population decline, this group is first to decrease, as floaters begin to fill vacancies when occurring. Undetected breeder replacement by floaters may mask a population decline; when the supply of floaters is exhausted, the breeding population may decline precipitously (Wilcove & Terborgh, 1984). Newton (1988) found that the favourable floater-to-breeder ratio is about 1:1 or greater. In buzzard populations, this group may consist of up to 3/4 of adult individuals (Kenward et al., 2000). Therefore, the observed apparent proportions of floaters (29% on Sakhalin Island and 21% on the Lower Amur) are comparatively low, and their temporal decrease may indicate population decline.

Conclusions

During the years of monitoring, we collected a large amount of data on the reproduction vital rates and population structure of Steller's Sea Eagles. Our results show that in both study areas the breeding efficiency is quite low, being even

lower on Sakhalin as compared to the Lower Amur. This suggests a possible decline of both Steller's Sea Eagle populations. This suggestion is supported by apparent changes in the population structure.

These results cause great concern about the future of both Steller's Sea Eagle populations. Further research and thorough analysis are required to guide conservation efforts to stabilise and recover the population.

Supporting Information

Structure and content of the database «Steller's Sea Eagle on Sakhalin Island and the Lower Amur, 2004–2019» (Electronic Supplement 1. Structure and content of the database «Steller's Sea Eagle on Sakhalin Island and the Lower Amur, 2004–2019») and the video of the brown bear predation of the Steller's Sea Eagle (Electronic Supplement 2. Brown bear attack on the Steller's Sea Eagle fledgling) may be found in the [Supporting Information](#).


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ЭФФЕКТИВНОСТЬ РАЗМНОЖЕНИЯ БЕЛОПЛЕЧЕГО ОРЛАНА НА ОСТРОВЕ САХАЛИН И В НИЖНЕМ ПРИАМУРЬЕ, РОССИЯ

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С середины 2000-х гг. мы проводили мониторинг состояния гнездящихся популяций *Haliaeetus pelagicus* (далее – орлан) на о. Сахалин (438 гнездовых территорий) и в низовьях р. Амур (Хабаровский край, 350 гнездовых территорий). Данные были собраны с 2004 по 2019 гг. в течение 12 полевых сезонов в каждом районе исследований. Основное внимание уделяли показателям эффективности размножения, главные из которых занятость гнездовых территорий, доля размножающихся пар, успех гнездования и размер выводка. Их сочетание определяет итоговое число потомков, которые произвела пара орланов на данной территории (продуктивность и, так называемая, производительность территории). Дополнительно мы рассматривали различные причины неудачного гнездования. Чтобы количественно охарактеризовать территориально-возрастную структуру популяции (долю молодых особей и долю нетерриториальных взрослых особей), мы регистрировали все встречи орланов. Наши исследования показывают, что все изученные характеристики сильно варьируют во времени и пространстве, в т.ч. и между регионами исследования. В целом эффективность размножения оказалась весьма низкой: средняя гнездовая территория на Нижнем Амуре производит 0.51 слетков в год, а на Сахалине еще меньше, 0.35 слетков в год. Средняя продуктивность на Сахалине также была меньше, чем на Нижнем Амуре: 0.51 и 0.62 слетков на занятую территорию в год, соответственно. Разница между регионами может объясняться хищничеством *Ursus arctos*, изымающих в среднем 18% потомства орланов на Сахалине (но не на Нижнем Амуре). Помимо прямого ущерба, хищничество *U. arctos* оказывает отложенное по времени воздействие на популяцию, влияя на занятость территорий и долю размножающихся пар на следующий год. Мы выявили два линейных временных тренда у сахалинской популяции: снижение доли размножающихся пар и увеличение смертности птенцов от прочих (не связанных с хищничеством) причин. Однако для окончательного объяснения низкой эффективности размножения орланов требуются дальнейшие исследования и более детальный анализ данных. Это позволит выработать адекватные природоохранные меры для стабилизации и восстановления обеих популяций орланов.

Ключевые слова: *Haliaeetus pelagicus*, *Ursus arctos*, бурый медведь, занятость территорий, мониторинг популяции, продуктивность, размер выводка, успех гнездования, хищничество медведей, чувствительные данные