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ESTIMATING THE NUMBER OF THE STELLER'S SEA EAGLE NESTING TERRITORIES USING ACCUMULATION CURVES

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Abstract. We developed an alternative approach to assessing raptor populations by fitting accumulation curves. This technique was applied to estimate the number of nesting territories of the Steller's Sea Eagle *Haliaeetus pelagicus* in the northeast of Sakhalin Island and the lower reaches of the Amur River (Russian Far East). From 2004 to 2021, 428 nesting territories were found on NE Sakhalin and 422 nesting territories on the lower Amur. We selected four asymptotic functions of accumulation curves (negative exponential, Clench, Weibull and Hill) and tested three different measures of sampling effort. The best model was the one based on the negative exponential function with an offset from the origin (known as the von Bertalanffy equation), with the number of nests visited as the measure of effort. This model suggested the existence of 461 nesting territories on NE Sakhalin and 535 nesting territories on the Lower Amur. Taking into account an average territory occupancy of 69 %, we estimated the breeding population to be 318.2 territorial pairs on NE Sakhalin and 480.4 pairs on the Lower Amur. The total population was estimated to be 1079.8 birds (including 896.2 adults and 183.6 immatures) on NE Sakhalin and 1414.1 birds (1216.1 adults and 198.0 immatures) on the Lower Amur. Our experience suggests that fitting accumulation curves is a useful tool for estimating raptor populations in long-term studies, especially when total counts are impossible and objects are unevenly distributed.

Keywords: accumulation curves, model, nesting territories, Steller's Sea Eagle, Haliaeetus pelagicus, Sakhalin Island, Amur River

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ОЦЕНКА ЧИСЛА ГНЕЗДОВЫХ ТЕРРИТОРИЙ БЕЛОПЛЕЧЕГО ОРЛАНА С ПОМОЩЬЮ КУМУЛЯТИВНЫХ КРИВЫХ

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Аннотация. Разработан альтернативный подход к оценке популяций хищников путем анализа кумулятивных кривых. Этот метод был применен для оценки количества гнездовых территорий белоплечего орлана *Haliaeetus pelagicus* на северо-востоке острова Сахалин и в нижнем течении реки Амур (Дальний Восток России). В период с 2004 по 2021 г. на северо-востоке Сахалина было обнаружено 428 гнездовых территорий, на нижнем Амуре – 422. Мы выбрали четыре асимптотические функции кумулятивных кривых (негативно-экспоненциальная, Кленча, Вейбулла и Хилла) и протестировали три различные меры поисковых усилий. Лучшей оказалась модель, основанная на негативно-экспоненциальной функции со смещением относительно начала координат (известной как уравнение Берталанфи) с числом посещенных гнезд в качестве меры усилий. Эта модель предполагает существование 461 гнездовой территории на северо-востоке Сахалина и 535 гнездовых территорий на Нижнем Амуре. Учитывая, что заселенность территорий составляет в среднем 69 %, мы оценили численность размножающейся популяции в 318,2 территориальных пар на северо-востоке Сахалина и 480,4 пар на Нижнем Амуре. Общая численность популяции оценивается в 1079,8 (включая 896,2 взрослых и 183,6 неполовозрелых) на северо-востоке Сахалина и 1414,1 птиц (1216,1 взрослых и 198,0 неполовозрелых) на Нижнем Амуре. Наш опыт показывает, что построение кумулятивных кривых является полезным инструментом для оценки численности популяций хищных птиц в ходе многолетних исследований, особенно когда полный учет невозможен, а объекты распределены в пространстве неравномерно.

Ключевые слова: кривые накопления, модель, гнездовые территории, белоплечий орлан, Haliaeetus pelagicus, остров Сахалин, река Амур

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Introduction

One of the main approaches to assessing breeding populations of large raptors is the count of their eyries or, in the case of territorial birds, nesting territories [1]. When the total count is impossible, for example, if the study area is large, researchers have to resort to extrapolations. In most cases these are spatial extrapolations [2], however, they do not always perform well, like in cases, when the space is heterogeneous [3, 4]. In this study, we apply another kind of extrapolation, based on fitting accumulation curves over time, to estimate the nesting population of a large raptor, the Steller's Sea Eagle (*Haliaeetus pelagicus*).

Two of the largest nesting populations of this species inhabit the northern part of Sakhalin Island and the lower reaches of the Amur River [5]. Their size is still not exactly known.

The first assessment of the Steller's Sea Eagle population on Sakhalin was made by Nechaev [6] who estimated it as "a little over 100 pairs" based on counts conducted in 1983–87. In the subsequent years, as the knowledge about the region increased, this estimate was repeatedly corrected, each time upwards. Thus, Masterov et al. (2000) developed a GIS-based logistic regression model which estimated eagle density in different habitats of the northeastern part of the island, most densely populated by the eagles. Using spatial extrapolation, this model predicted the existence of 434 nesting territories in this area. There is also an expert estimation of the number of nesting territories on the entire island: 550–570 [7]. Estimates of the Amur Steller's Sea Eagle population have not been made so far.

In 2004, when our long-term monitoring program started on the NE Sakhalin Island and two years later on the Lower Amur, the database of known nesting territories was created. Initially, it has 175 records for the island and 110 records for the mainland, but every field season this number continuously grew, reaching 428 and 422 nesting territories by 2021, respectively.

The dynamics of this growth, when plotted, produce an accumulation curve whose shape implies that it asymptotically approaches a certain limit, which is the true number of nesting territories in the study area. To obtain this number, we developed a model that estimates the asymptote by fitting the accumulation curves.

Accumulation curves are useful and widely used tools for prediction and extrapolation in ecological research. Most commonly they (referred to as species accumulation curves) are used to assess the richness and diversity of species (or other taxa) (e.g., [8–12]). Hence the definition of the "species accumulation curve" or "collector's curve" given by [13] as a graph reflecting the accumulated number of species as a function of the number of search efforts. A similar application is an estimation of genetic diversity (e.g., [14]. Deng et al. [15] demonstrated the applicability of accumulation curves in a broader context, ranging from linguistics to molecular biology). These applications include studies of animal behavioural repertoires [16–18], corpus linguistics analysis [19, 15], dynamics of magazine readership [20], and quantification of the size distribution of plant roots [21].

In this study, we test the usability of accumulation curves for estimating raptor populations, specifically, the number of nesting territories of the Steller's Sea Eagles. Our purposes were: to compare the performance of different accumulation curve models and effort measures, and select the best one; to estimate the true number of eagle nesting territories within two study areas; to determine the sampling effort required to catch a nominated percentage (e.g. 95 %) of the predicted number of nesting territories in the study area.

Study object, the Steller's Sea Eagle

Our study object is the Steller's Sea Eagle *Haliaeetus pelagicus* (Pallas 1811), a vulnerable raptor species whose global population is estimated by different sources at 3600–4670 individuals [22] and 6000–7000 individuals [5]. Due to its limited breeding range, which does not extend beyond the Russian Far East and its naturally low productivity, the species is classified as globally threatened (vulnerable) in the IUCN Red List [22], listed in the Red Book of the Russian Federation [23], and protected by a number of international conventions and bilateral agreements.

Steller's Sea Eagles are large birds of prey that inhabit the coasts of the Sea of Okhotsk and adjacent areas. Since the diet of this species consists substantially of fish and other aquatic and semi-aquatic animals, its life cycle is tightly associated with the sea coasts and freshwater reservoirs. In forested landscapes, such as the study areas, these eagles nest mainly in trees, and their main nesting habitats are forested tracts and forest fragments situated not far from water bodies. In some other parts of the range (Kamchatka and the northern part of the Sea of Okhotsk) they also nest on cliffs and rocks.

Sea eagles' nests are large, usually prominent structures about 1.5–2 m wide, made of branches and normally placed in the upper part or on the top of the tree.

Quite often a pair of sea eagles build several nests, among which they choose one for breeding, while others (called *alternate*, or *alternative nests*) are either used for other purposes (perching, eating, *etc.*) or go unused in a given year. That is why a researcher should focus on *nesting territories* rather than individual nests [1]. Sea eagles occupy territories for many years, and their nesting territories can persist for decades, which makes them useful for indirect counts of sea eagle populations [24, 25].

Following Steenhof et al. [26], we understand a nesting territory as an area that contains, or historically contained, one or more nests within the home range of a mated pair: a confined locality where nests are found, usually in successive years, and where no more than one pair is known to have bred at one time. Steller's Sea Eagle nesting territories may not include all of a pair's foraging habitat [27] (Fig. 1).

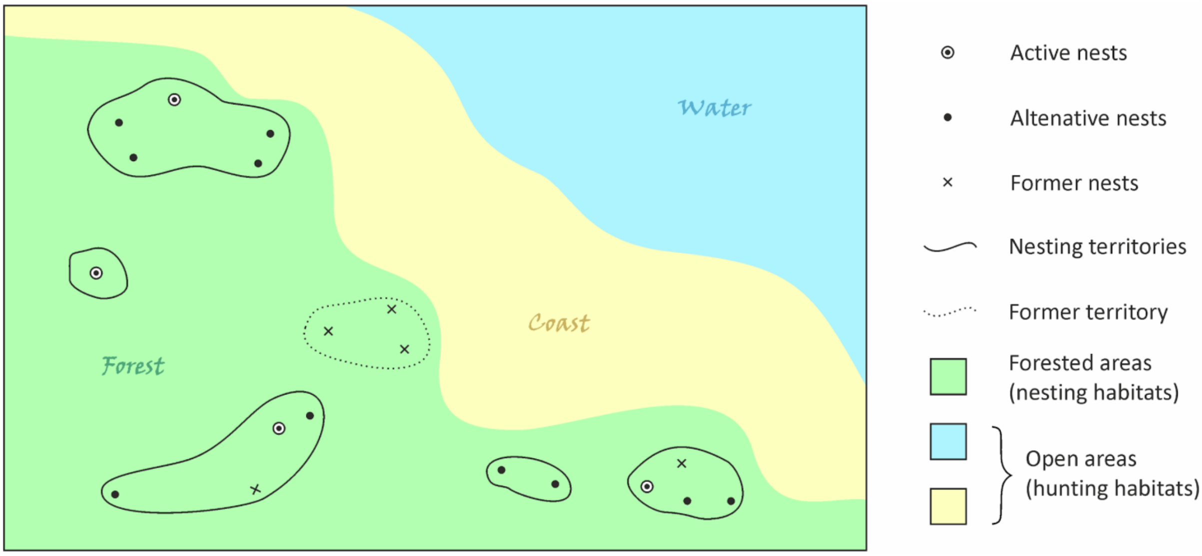

Fig. 1. Nesting territories of Steller's Sea Eagles (a scheme). Six territories are shown, of which four are active (have an active nest with eggs or nestlings), one is not active and one is no longer in existence

Study area

The field studies were conducted in two regions of the Russian Far East, Sakhalin Island (Sakhalin Region) and the lower reaches of the Amur River (Khabarovsky Krai). Thus, there are two study areas on the island and on the continent, named "Sakhalin" and "Lower Amur", respectively (Fig. 2).

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°23'57" N and 51°11'14" 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. Considering only the area that is potentially suitable for sea eagles, the study area covers 3280 km^2.

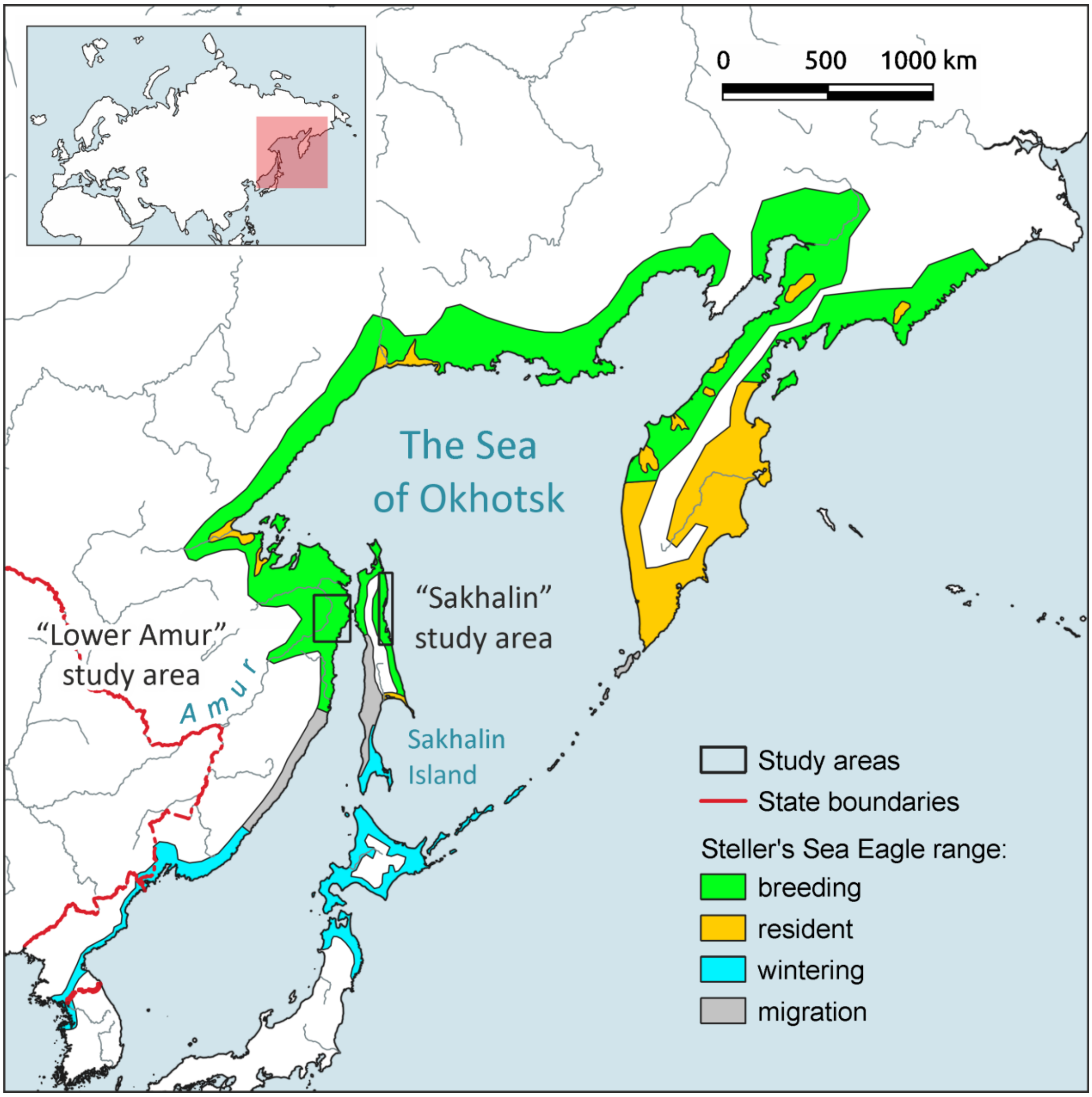

Fig. 2. The Steller's Sea Eagle global range and two study areas, "Lower Amur" (Khabarovsky Krai) and "Sakhalin" (Sakhalin Region)

The "Lower Amur" study area comprises the lower reaches of the Amur River, including the channels of the Amur floodplain and associated large and small lakes and their tributaries. 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 boundary runs along the Pilda River (139.5° E), and the eastern boundary is the coast of the Tatar Strait. The total area is about 4000 km^2. Coordinates of the rectangle covering the two study areas: 51.1° E and 53.7° E latitude, 139.5° N and 143.7° N longitude.

The most common raptor in the study area is the Steller's Sea Eagle, which accounts for over 95 % of all raptor sightings. The next in abundance is the White-tailed Eagle *Haliaeetus albicilla*, which is much less numerous (less than 5 % of sightings), but still is not uncommon. The important fact is that these two sea eagle species share similar habitats and can occupy each other's nests and nesting territories. Other birds or prey are exceptionally rare in the study area. These are the Goshawk *Accipiter gentilis* (one known territory), the Osprey *Pandion haliaetus* (several observations, no nests found), and Eastern Buzzard *Buteo japonicus* (bird observations, no nests found). Nests of these species are not used by the Steller's Sea Eagle, so we do not consider them in this study.

Data collection

Field studies were conducted from 2004 to 2021 (including 2004–2014, 2018, 2019 on Sakhalin, and 2006–2010, 2012–2018, 2021 on the Lower Amur). The main fieldwork was carried out from the beginning of July to the end of August. This time of the breeding season is the period of least vulnerability of Steller's Sea Eagles when visiting nesting sites is the least disturbing for them [5]. At this time, grown nestlings are still in the nests preparing to fledge, which usually occurs in the second decade of August. In some years we have been able to conduct additional spring counts in the Sakhalin study area in April. At this time of the year, the bays and rivers of northeastern Sakhalin are covered with ice, making some remote areas more accessible by snowmobile. Spring counts were conducted in 2005–2010, 2014 and 2019.

During the field works we combed the study area, inspected known Steller's Sea Eagle and White-tailed Eagle nests, and searched for new nests. Then nests were grouped into nesting territories on the basis of territorial proximity, taking into account their occupancy status. For the White-tailed Eagle, we only included nests and territories that had ever been used by Steller's Sea Eagles.

As a general criterion for nest proximity, we used the doubled radius of the area around the nest defended by territory holders, which is approximately 400 m [28]. We also took into account the distribution and territorial behaviour of the birds. For example, if we observed two territorial pairs or detected two breeding attempts in what was presumed to be one nesting territory, it was divided into two nesting territories belonging to different pairs. A nesting territory usually contains 1–2 nests on the Lower Amur and 1–3 nests on Sakhalin, but sometimes, especially on Sakhalin, there are up to 13 nests (including unfinished and destroyed ones). The average number of nests per nesting territory is 1.5 on the Lower Amur and 2.9 on Sakhalin [5].

Each field season, we kept finding new nests and nesting territories, which were added to the database. After 13 field seasons in each study area, we obtained two accumulation curves corresponding to the incremental growth in the number of known nesting territories.

Database construction

A relational database was developed in MS Access for data entry, storage, manipulation and extraction for subsequent statistical processing and spatial analysis. The main data included in the database was information on the location and condition of nests and nesting territories, their status in different years, and also observed individuals of the Steller's Sea Eagle. The database therefore essentially consists of five interrelated tables: Nests, Territories, Nest status, Territory status, and Birds [29].

The peculiarity of the database is that when monitoring began in 2004, some nests and nesting territories were already known, and their coordinates were recorded in field diaries and Excel spreadsheets, which served as the basis for the database creation. This means that by the time $t = 0$ some search effort had already been made, which should be taken into account in the choice of model.

Models tested

Following Colwell & Coddington [13], we understand an accumulation curve (with the correction to the subject of our research) as the number of nesting territories found plotted as a function of some measure of the sampling effort expended to find them.

The samples of nesting territories were taken once a year. To construct the accumulation curve, we added successive samples together, so that the y-axis measures the cumulative pooled series of samples. This approach is called a "sample-based protocol" [30].

In general, there are dozens of different functions used to fit accumulation curves [11]. However, not all of them fit the conditions of our study. First, since the ecological capacity of the environment is finite, the accumulation curve necessarily has a limit, which is the true number of nesting territories in the study area. Therefore, only asymptotic functions [8] should be considered. Secondly, at time zero, when the monitoring programme started (in 2004 on Sakhalin Island and 2006 on the Lower Amur), some nesting territories were already known which means that at the time $x = 0$ the amount of effort $F(x) > 0$. So, the function should not necessarily cross the origin. If it does, we add the additional parameter β, the offset from the origin. In practice, this means the amount of effort expended before the start of the monitoring. Furthermore, we did not consider sigmoidal functions (such as logistic ones) because of the nature of our accumulation curves, which look completely concave and do not seem to have any inflexion points. In the end, we selected four models that met these requirements: Bertalanffy, Clench, Hill, and Weibull. There are other models, but they describe exactly the same functions.

Bertalanffy model

This model is essentially an extension of the negative-exponential model with an offset from the origin (β). It has the following equation:

$$F(x) = N\left(1 - exp\left(-\alpha\left(x + \beta\right)\right)\right), \tag{1}$$

where x is the amount of effort, N is the asymptote, α is a fitted constant that controls the shape of the curve, and β is the amount of previous effort.

When β = 0, this function becomes the negative-exponential equation, which is widely used to fit accumulation curves [13, 31, 9]. The negative exponential assumes that the probability that the next individual represents a new species depends linearly on the current size of the species list, and decreases to zero as the asymptote is approached [13].

The 3-parameter Bertalanffy model is often referred to as the "von Bertalanffy function" [32], but there there are at least six other 3-parameter equations that describe exactly the same negative-exponential function with an offset from the origin and can be converted to each other by reparametrisation [33]. These equations are used in various fields of ecology and economics, such as modelling fish body growth, forest growth, and fertiliser efficiency, and also in palaeontology to model shell growth [34]. The offset corresponds to the non-zero size of a fish at age 0 (the moment of hatching from the egg), or the non-zero yield of crops with no fertiliser added, etc.

Clench model (with an offset)

The next model tested is the Clench model [35], is described by the two-parameter function

$$F(x) = Nx/(\alpha + x), \tag{2}$$

where N is the asymptote, α is a second parameter controlling the shape of the curve, and x is the amount of effort. The Clench model is based on the Michaelis-Menten equation, which was originally invented to describe enzyme kinetics [36], hence it is also known as the Michaelis-Menten model [37]. In a reparameterised form, this function, known as the Yield-loss model, is used applied in agronomy to model yield loss to weed density [38].

Since the Michaelis-Menten equation necessarily passes through the origin, we add a third parameter, β, the offset:

$$F(x) = N(x+\beta)/(\alpha + x + \beta), \tag{3}$$

Weibull model

This model is based on the cumulative Weibull distribution as a non-parametric estimator of total species richness [9, 39]. This model has four parameters:

$$F(x) = N\left[1 - exp\left(-\alpha(x+\beta)^{\gamma}\right)\right], \tag{4}$$

where x is the effort, and parameters N is the asymptote, α, β, γ are the parameters obtained by the model (at this β is the offset from the origin).

Hill model

This model was originally developed to quantify oxygen dissociation curves [40], and its application to the fitting of species accumulation curves was approved by Thompson et al. [11]. It is a 3-parameter function:

$$F(x) = N\left(\alpha(x+\beta)^{\gamma}\right)/\left(1+\alpha(x+\beta)^{\gamma}\right), \tag{5}$$

where N is the asymptote, α and γ are slope and shape parameters, β is the offset from the origin (amount of previous effort).

Measuring sampling effort

The samples of nesting territories were collected on an annual basis. To construct the accumulation curve, successive samples were added so that the x-axis measures the cumulative pooled series of samples. This approach is referred to as a "sample-based protocol" [30].

The choice of an appropriate measure of sampling effort is a separate issue. Sometimes researchers use multiple measures (e.g. [11]). In this study, we used three measures of sampling effort. The simplest measure of sampling effort could be the cumulative number of samples, or, equivalently, the *number of field seasons*. However, the amount of fieldwork varied between years due to differences in the scope of fieldwork, weather conditions and logistical constraints. To account for these differences, we also measured the effort in terms of the *number of field days*. Again, this measure may not be perfect because of the differences in weather conditions between days. For example, on different days we managed to visit between 1 and 60 nests. Therefore, we chose the *number of nests visited* as a third measure of effort.

Statistical methods

All calculations were performed in the R statistical software environment [41]. Models were fitted to the data using the *nls* and *nlsLM* functions of the standard R package. These functions use the Gauss-Newton algorithm to fit a user-defined equation to the data and produce parameter estimates along with their standard errors.

Standard goodness-of-fit criteria including mean squared error (MSE), adjusted coefficient of multiple determination (R^2 adj.), and a graphical examination of residuals were used to assess model performance, as recommended by Draper & Smith [42]. The adjusted R^2 was used as it takes into account varying number of parameters in different models, allowing us to compare the performance of different non-linear models [43].

Results

After 13 field seasons in each study area we found 428 Steller’s Sea Eagle nesting territories on

Sakhalin and 422 on the Lower Amur (Table 1). The sampling effort varied greatly between years in terms of field days and nests visited. Although the study period was very long, we never stopped finding new territories, and never reached the level of redundancy [44]. However, the rate of discovery decreased over the years, suggesting that the majority of nesting territories had already been found.

Table 1

Dynamics of accumulation of found nesting territories (from field data)

Year	Current effort			Accumulated effort (*x*)			Accumulated number of territories (*y*)
	field seasons	field days	visited nests	field seasons	field days	visited nests	
NE Sakhalin							
2004	1	62	312	1	62	312	175
2005	1	54	441	2	116	753	214
2006	1	55	575	3	171	1328	240
2007	1	50	635	4	221	1963	283
2008	1	54	720	5	275	2683	303
2009	1	57	888	6	332	3571	342
2010	1	56	930	7	388	4501	360
2011	1	26	552	8	414	5053	367
2012	1	24	411	9	438	5464	382
2013	1	26	474	10	464	5938	387
2014	1	43	778	11	507	6716	401
2018	1	20	83	12	527	6799	402
2019	1	43	934	13	570	7733	428
Lower Amur							
2006	1	15	142	1	15	142	110
2007	1	13	120	2	28	262	122
2008	1	9	44	3	37	306	129
2009	1	17	104	4	54	410	133
2010	1	19	259	5	73	669	181
2012	1	11	174	6	84	843	241
2013	1	16	250	7	100	1093	256
2014	1	13	204	8	113	1297	267
2015	1	1	43	9	114	1340	288
2016	1	36	464	10	150	1804	361
2017	1	33	317	11	183	2121	381
2018	1	44	466	12	227	2587	396
2021	1	32	490	13	259	3077	422

Visual examination of the accumulation curve, as recommended by Thompson et al. (2003) shows that it does not plateau, despite considerable trapping effort (Fig. 3).

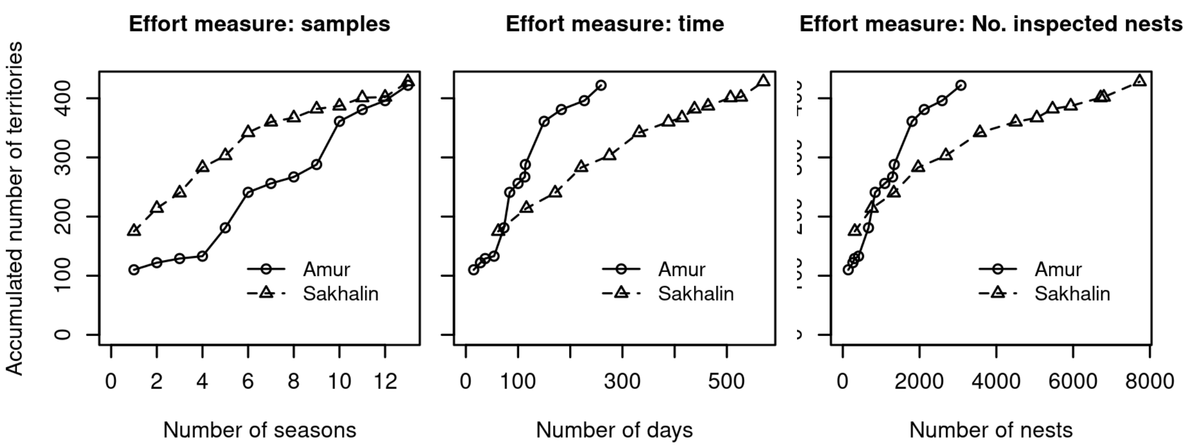

Fig. 3. Accumulation curves for Sakhalin Island and the Lower Amur, constructed from field data. There are three measures of sampling effort: the number of samples (the number of field seasons), time (the number of field days) and sample volume (the number of inspected nests)

Four functions per three effort measures per two study areas produce 24 different models which we fitted to the field data. The results of the modelling are shown in Table 2.

Table 2

Estimation of the asymptote by 4 different models

Model	Effort measure	N	± SE	α	β	γ	adj. R^2
NE Sakhalin							
Bertalanffi	Seasons	460.3	± 14.5	0.162	1.857	–	0.990
	Field days	578.0	± 39.5	1.88×10^{-3}	127.8	–	**0.995**
	Visited nests	461.1	± 1.38	2.48×10^{-4}	1689	–	0.993
Clench	Seasons	594.9	± 33.8	5.874	1.3393	–	0.989
	Field days	842.8	± 82.5	676.7	112.9	–	**0.995**
	Visited nests	585.8	± 23.8	3593.1	1251.4	–	**0.995**
Hill	Seasons	462.2	± 47.9	1.3×10^{-3}	2.979	6.912	0.991
	Field days	691.4	± 359.3	2.5×10^{-4}	1.325	168.2	**0.995**
	Visited nests	1029.2	± 1012	6.8×10^{-3}	0.5138	452.0	**0.995**
Weibull	Seasons	434.8	± 24.0	5.79×10^{-2}	1.4219	3.599	0.982
	Field days	533.6	± 127.5	6.7×10^{-4}	1.175	166.8	**0.995**
	Visited nests	767.4	± 603.4	1.24×10^{-2}	0.4624	402.8	**0.995**
Lower Amur							
Bertalanffi	Seasons	–	–	–	–	–	–
	Field days	580.5	± 102.1	4.98×10^{-3}	16.45	–	0.956
	Visited nests	534.6	± 50.3	4.89×10^{-4}	261.0	–	**0.982**
Clench	Seasons	–	–	–	–	–	–
	Field days	911.8	± 241.9	299.1	15.78	–	0.958
	Visited nests	789.2	± 114.5	2717.25	230.41	–	**0.982**
Hill	Seasons	943.6	± 219.2	2.3×10^{-5}	3.236	1.275	0.972
	Field days	499.9	± 136.7	8.8×10^{-8}	3.05	108.7	0.969
	Visited nests	542.5	± 158.5	4.4×10^{-7}	1.933	748.6	**0.984**
Weibull	Seasons	601.7	± 566.9	1.7×10^{-5}	3.393	13.98	0.972
	Field days	424.4	± 26.55	2.5×10^{-7}	2.800	120.7	0.973
	Visited nests	443.7	± 38.76	1.3×10^{-6}	1.775	834.1	**0.986**

Although the adjusted coefficient of determination (adj. R^2) for all models was quite high (at least 0.95), the range of asymptote estimates proved to be large: estimates of the number of nesting territories ranged from 434.8 to 1029.2 for the northern Sakhalin, and from 424.4 to 943.6 for the on Lower Amur. However, most of the estimates for Sakhalin (eight of the 12) are aggregated between 434.8 and 594.9, and between 424.4 and 580.5 for the Lower Amur (six of the 10).

Of the three measures of effort, the number of visited nests was the best, the number of field days was almost as good, and the number of field seasons was the worst. The two models for the Lower Amur, the Bertalanffy and Clench models, never converged.

Difference between the Sakhalin and the Lower Amur accumulation curves

The cumulative curves constructed from the Lower Amur and Sakhalin field data (Fig. 3) differ in character. The Amur curve starts with lower values but eventually catches up with the Sakhalin curve. The growth rate of the Lower Amur curve is significantly higher, especially in models where the measure of effort is the number of field days or visited nests. As a result, the Lower Amur has almost as many territories as Sakhalin, despite half the effort (in terms of field days and the number of visited nests). A possible explanation for this difference is the different structure of Steller's eagle territories in the study areas. For example, in the Lower Amur, a nesting territory usually consists of one or two nests (an average of 1.5 nests per territory), whereas on Sakhalin a territory may contain up to 10 or more nests (including unfinished and destroyed nests).

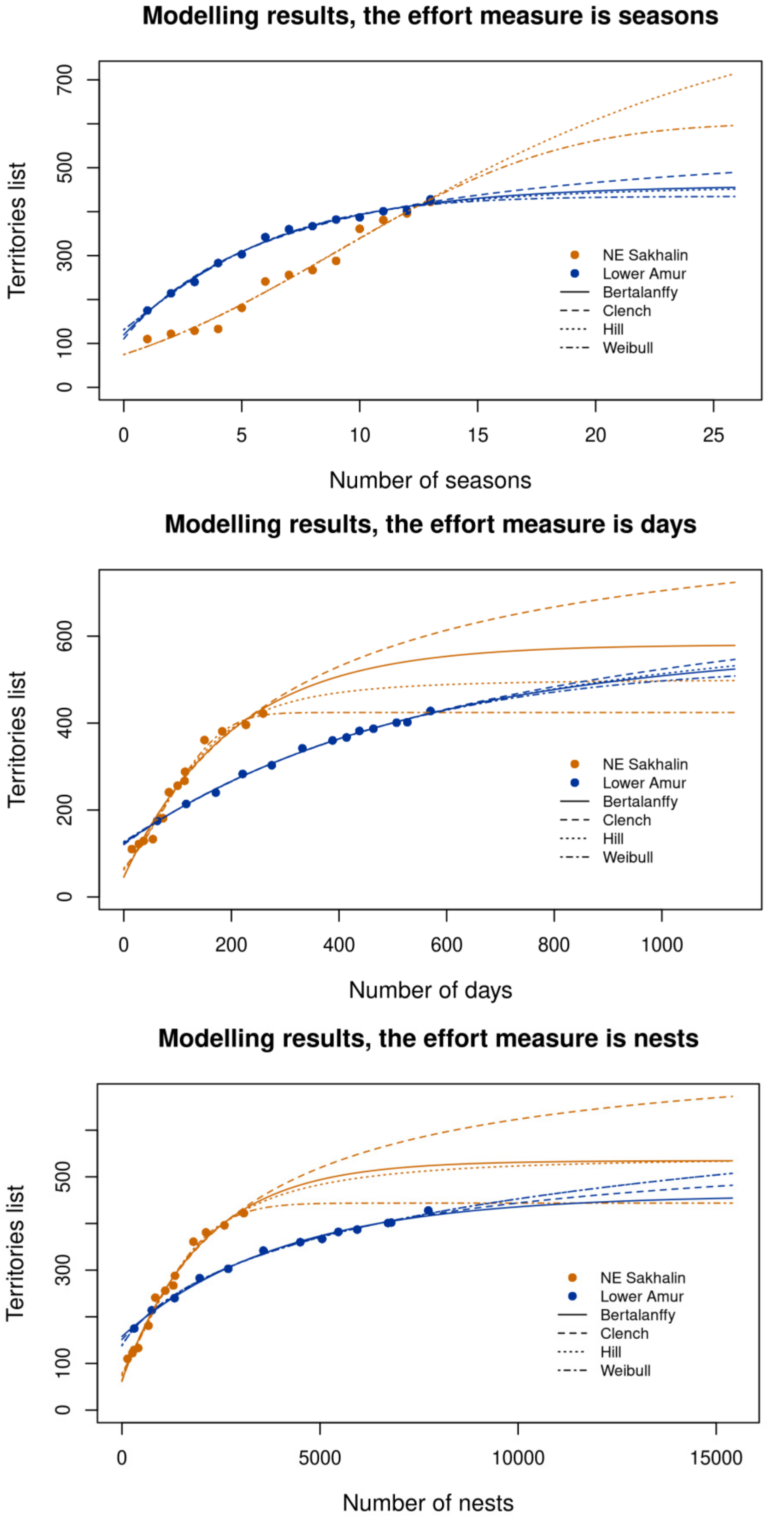

Fig. 4. Solid lines represent the Bertalanffy model, dashed lines are the Clench model, dotted lines are the Hill model, and long-dashed lines are the Weibull model. Measures of effort are the number of samples (or field seasons), the number of field days, the number of visited nests

This difference in structure is in turn explained by the higher level of anthropogenic disturbance on Sakhalin, which is now an intensively developed region where oil and gas fields are being actively exploited. This results in eagles making fewer nesting attempts and replacing them with nest-building activity. This situation is exacerbated by high predation pressure from brown bears, which not only eat chicks but also destroy nests [45], forcing eagles to be more active in repairing old nests and building new ones.

Another possible explanation is the different landscape character of the study area, which makes it easier to find eagle nests and territories in the Lower Amur. In any case, this question requires a separate study.

Choosing the best model and effort measure

Our 22 models, fitted to the curves (12 for Sakhalin and 10 for Amur), showed more than twice the range of the asymptote estimates. At the same time, the coefficient of determination (adjusted R^2) for all of them was quite high, no less than 0.95. In this situation, it makes sense to choose the model that is the most consistent from a biological point of view.

Of the three different units of effort, the one we like best is the number of visited nests. In fact, the number of field seasons is too coarse a measure, as the samples collected in different years vary considerably in size. The number of days in the field is a better reflection of the amount of fieldwork but is not an optimal measure either. Depending on weather conditions and logistical constraints, we were able to visit anywhere from 1 to 60 nests on different days, i.e. individual days can vary considerably in terms of the amount of fieldwork done.

Moreno & Halffter [46], who studied the problem of choosing an appropriate measure of effort, came to the conclusion that the best candidate for this role is the very object the researcher is dealing with. When constructing species curves, such objects are individuals belonging to different species. For example, Gotelli & Colwell [30] note that, ideally, units of effort should be based on the accumulated number of individuals because the carriers of taxonomic information are individuals. Furthermore, when analysing a corpus of text, one is dealing with individual word entries. In our case, the fieldwork was focused on individual nests belonging to specific nesting territories. Therefore, from this point of view, the best measure of effort is the number of visited nests.

Regarding the choice of model, researchers recommend that, in cases of doubt, the most logical and biologically consistent model should be chosen.

We prefer the Bertalanffy model as the simplest of the four tested models. It is based on a negative-exponential function, which, in turn, can be derived directly from a simple assumption that the efficiency (qualification, experience) of census takers does not change and the rate of finding new nesting territories is negatively proportional to the number of territories found. That is why this model is also called the linear dependence model [8, 47, 11]. The Bertalanffy function differs from it only in the presence of a shift from the origin, which, as we have already said, is connected with the presence of previous efforts. Each of the three parameters of the model has a physical meaning: N is the true number of nesting territories, α is a constant that determines the effectiveness of search efforts, and β is the number of the previous search effort.

The Weibull and Hill models have a significant drawback: they sometimes take a sigmoid form, as can be seen in Fig. 4 (top). This means that the rate of discovery of new territories first increases and then decreases, which does not correspond to real data. In reality, the rate at which nesting territories were discovered was the fastest at the beginning. Thus, these two models do not describe very well the nature of the objects we study.

The remaining, Clench model, was originally developed to describe chemical reactions. In particular, it describes how the rate of conversion of the enzyme-substrate complex into a product slows down as the concentration of the product increases. It is not clear, however, how the parameters of this model relate to the process of territory finding. Compared to the Bertalanffy model, the Clench model produces higher estimates of the asymptote.

Therefore we retained two of the four models and compared them with the previous estimate from the GIS-based regression model for NE Sakhalin [48]): 434 nesting territories, which is closer to the results of the Bertalanffy model (461.1 territories) and further away from the estimate of the Clench model (585.8 territories). Furthermore, the Bertalanffy model is in better agreement with the previous estimate of Masterov et al. [5] for the whole of Sakhalin: 550–570 territories.

Taking the Bertalanffy model at face value, we suggest that the knowledge of the study area on Sakhalin is about 93 % (428 of 461 territories are known), which corresponds to the desirable level of completeness of 90 % recommended for accumulation curves (Moreno & Haffner 2000, Taylor *et al*. 2013). For the Lower Amur, the knowledge of the study area is about 79 % (422 out of 535 territories are known), which is below the desired level of completeness.

From these figures, we can proceed to asses the population numbers of eagles in the two study areas. It is important to remember that not all territories are occupied. After correcting for the territory occupancy, which averages 69 % [29], we estimate the breeding population of this species on the northeastern Sakhalin at 318.2 territorial pairs, or 636.3 territorial birds (Table 3). According to [29], the proportion of floaters in adult birds equals

0.29, and the proportion of immatures is 0.17 (correspongingly, the proportion of adults is 0.83). From these figures, we estimate the total number of adults to be 636.3 / 0.69 = 896.2 individuals (including 636.3 territorial birds and 259.9 floaters). The total population is 896.2 / 0.83 = 1079.8 individuals, of which 183.6 are immatures.

Table 3

Calculation of the population size from the estimates of the asymptote and the population structure

Parameter	NE Sakhalin	Lower Amur
Asymptote estimate	461.1	585.8
Territory occupancy	0.69	0.82
Proportion of floaters in adult birds	0.29	0.21
Proportion of immatures	0.17	0.14
Number of occupied territories	318.2	480.4
Number of territorial birds	636.3	960.7
Number of floaters	259.9	255.4
Number of all adults	896.2	1216.1
Number of immatures	183.6	198.0
Total population	1079.8	1414.1

Similarly, we estimate the population of the Lower Amur study area to be 1414.1 individuals, including 1216.1 adults (of which 960.7 are "breeders" and 255.4 are floaters) and 198.0 immatures.

Conclusions

We conclude that accumulation curves can be useful for assessing raptor populations. This approach may be useful in long-term studies, especially in cases where habitats are patchy and a population is unevenly distributed in space, making spatial extrapolation difficult.

Of all the possible asymptotic models, the most useful proved to be the negative-exponential model, which we used with a shift around the origin that transformed it into the Bertalanffy model. This is a fairly simple model, whose parameters are easy to interpret, and which is in good agreement with previous estimates and models.

The use of cumulative curves is especially promising in cases where the study area is very large in area and it is impossible to make an absolute count, especially when the objects under study are unevenly distributed in space.

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