Conservation Biology

Conservation Methods

Optimization of capture–recapture monitoring of elusive species illustrated with a threatened grasshopper

Linda Bröder,[1]* Laurent Tatin,[2] Axel Hochkirch,[1] Andreas Schuld,[1] Lucas Pabst,[1] and Aurélien Besnard[3]

[1]Department of Biogeography, Trier University, Universitätsring 15, 54296, Trier, Germany
[2]Conservatoire d'espaces naturels de Provence-Alpes-Côte d'Azur, 2 Place Léon Michaud, 13310, Saint Martin de Crau, France
[3]EPHE, PSL Research University, CNRS, UM, SupAgro, IRD, INRA, UMR 5175 CEFE, Centre d'Ecologie Fonctionnelle et Evolutive, Campus CNRS - 1919 route de Mende, 34293, Montpellier, France

Abstract: Information on population sizes and trends of threatened species is essential for their conservation, but obtaining reliable estimates can be challenging. We devised a method to improve the precision of estimates of population size obtained from capture–recapture studies for species with low capture and recapture probabilities and short seasonal activity, illustrated with population data of an elusive grasshopper (*Prionotropis rhodanica*). We used data from 5 capture–recapture studies to identify methodological and environmental factors affecting capture and recapture probabilities and estimates of population size. In a simulation, we used the population size and capture and recapture probability estimates obtained from the field studies to identify the minimum number of sampling occasions needed to obtain unbiased and robust estimates of population size. Based on these results we optimized the capture–recapture design, implemented it in 2 additional studies, and compared their precision with those of the nonoptimized studies. Additionally, we simulated scenarios based on thresholds of population size in criteria C and D of the International Union for Conservation of Nature (IUCN) Red List to investigate whether estimates of population size for elusive species can reliably inform red-list assessments. Identifying parameters that affect capture and recapture probabilities (for the grasshopper time since emergence of first adults) and optimizing field protocols based on this information reduced study effort (−6% to −27% sampling occasions) and provided more precise estimates of population size (reduced coefficient of variation) compared with nonoptimized studies. Estimates of population size from the scenarios based on the IUCN thresholds were mostly unbiased and robust (only the combination of very small populations and little study effort produced unreliable estimates), suggesting capture–recapture can be considered reliable for informing red-list assessments. Although capture–recapture remains difficult and costly for elusive species, our optimization procedure can help determine efficient protocols to increase data quality and minimize monitoring effort.

Keywords: capture probability, IUCN Red List, monitoring, population size

Optimización del Monitoreo de Captura y Recaptura de Especies Esquivas Ilustrado con un Saltamontes Amenazado

Resumen: La información sobre los tamaños poblacionales y las tendencias de las especies amenazadas es esencial para su conservación, pero la obtención de estimaciones confiables puede ser todo un reto. Diseñamos un método para mejorar la precisión de las estimaciones del tamaño poblacional obtenidos de estudios de captura y recaptura para especies con probabilidades bajas de captura y recaptura y una corta actividad estacional y lo ilustramos con los datos poblacionales de un saltamontes esquivo (*Prionotropis rhodanica*). Usamos los datos de

*Address correspondence to Linda Bröder, email: linda.broeder@mailbox.org
Article impact statement: *Optimization helps minimize efforts to obtain reliable data from capture-recapture studies of elusive species to inform conservation.*
Paper submitted May 25, 2019; revised manuscript accepted November 29, 2019.

Conservation Biology, Volume 34, No. 3, 743–753

DOI: 10.1111/cobi.13449

cinco estudios de captura y recaptura para identificar los factores metodológicos y ambientales que afectan a la probabilidad de captura y recaptura y a los estimados de tamaños poblacionales. En una simulación, usamos el tamaño poblacional y las estimaciones de probabilidad de captura y recaptura obtenidos en estudios de campo para identificar el número mínimo de ocasiones de muestreo necesarias para obtener estimaciones imparciales y sólidos del tamaño poblacional. Con base en estos resultados, optimizamos el diseño de la captura y recaptura, la implementamos en dos estudios adicionales y comparamos su precisión con aquella de los estudios no optimizados. Además, simulamos escenarios con base en los umbrales de tamaño poblacional localizados en los criterios C y D de la Lista Roja de la Unión Internacional para la Conservación de la Naturaleza (UICN) para conocer si las estimaciones del tamaño poblacional para especies esquivas pueden informar certeramente las valoraciones de lista roja. La identificación de los parámetros que afectan las probabilidades de captura y recaptura (desde el momento de aparición de los primeros saltamontes adultos) y la optimización de los protocolos de campo con base en esta información redujeron el esfuerzo de estudio (−6% a −27% ocasiones de muestreo) y proporcionaron estimaciones más precisas del tamaño poblacional (coeficiente reducido de variación) en comparación con los estudios no optimizados. Las estimaciones del tamaño poblacional tomadas de los escenarios basados en los umbrales de la UICN fueron, en su mayoría, imparciales y sólidos (sólo la combinación de poblaciones muy pequeñas y un esfuerzo mínimo de estudio produjo estimaciones no confiables), lo que sugiere que la captura y recaptura puede considerarse como confiable para informar las valoraciones de lista roja. Aunque la captura y recaptura todavía es complicada y costosa cuando se aplica a especies esquivas, ésta puede ayudar a determinar los protocolos eficientes para incrementar la calidad de los datos y minimizar el esfuerzo de monitoreo.

Palabras Clave: Lista Roja UICN, monitoreo, probabilidad de captura, tamaño poblacional

摘要: 受威胁物种的种群大小及变化趋势的信息对其保护至关重要, 但获得这些信息的可靠估计却是一项挑战。我们设计了一种方法来提高利用重捕法评估那些捕获率和重捕率低, 季节性活动短的物种的种群大小的精度, 并应用一种难以观察的蝗虫 (*Prionotropis rhodanica*) 的种群数据为例进行了验证说明。主要利用5个捕获-重捕研究的数据确定了影响捕获率、重捕率和种群大小估计的方法学及环境因素, 并用野外研究估计的种群大小、捕获率和重捕率模拟确定了获得无偏且稳健的种群大小估计所需的最小采样次数。基于这些结果, 我们优化了捕获-重捕设计并在另外两个研究中进行了测试, 并比较了优化后的精度与未优化研究的精度的差异。此外, 我们还根据《国际自然保护联盟 (IUCN) 红色名录》标准 C 和 D 中的种群大小阈值做了情景模拟, 以分析对难观测物种的种群大小估计是否能为红色名录评估提供可靠信息。结果显示, 确定影响捕获率和重捕率的参数 (对于蝗虫来说是成体首次出现以来的时间) 并基于这些信息来优化野外实践方法, 相比于未优化的研究可以减轻研究工作量 (−6%到−27%的采样次数) 并提供更精确的种群大小估计 (减小变异系数) 。而基于 IUCN 阈值的情景获得的种群大小估计大多无偏且稳健 (只有种群很小且研究工作量很低的组合估计结果不可靠), 这表明重捕法可以用于为红色名录评估提供信息。虽然重捕法对于难观测物种来说仍然是具有困难且成本较高, 但我们的优化方法可以帮助确定更高效的实验操作, 以提高数据质量并减少种群监测的工作量。**【翻译: 胡怡思; 审校: 聂永刚】**

关键词: 捕获概率, IUCN 红色名录, 监测, 种群大小

Introduction

Robust estimates of population sizes are essential for assessing the conservation status of threatened species and for testing the efficacy of conservation strategies (Sutherland et al. 2004). Obtaining reliable estimates based on an appropriate sampling design is a key element of monitoring (Yoccoz et al. 2001), but can be challenging, particularly for elusive species (Thompson 2004) (i.e., species that are difficult to detect). Monitoring of species with low detection probabilities often requires a huge field effort that may result in sparse data. Thus, elusive species may be neglected in conservation practice and research, regardless of their extinction risk, or incorrect management decisions may be made (Chadès et al. 2008).

Several approaches have been developed to obtain robust monitoring data for species with low detection rates (e.g., Willson et al. 2011; Dénes et al. 2015; Specht et al. 2017). However, these approaches mainly target occupancy rates or dynamics, which do not allow estimating some key parameters of conservation interest, such as abundance, survival, immigration, or emigration. Capture–recapture (Nichols 1992; Pollock 2000) is the most powerful way to obtain unbiased population parameter estimates when detection probability is <1. Yet, like other methods, capture–recapture is difficult to apply to elusive species because low detection probabilities result in low capture and recapture rates. The consequent small sample sizes may provide unreliable or biased estimates (White 1982). To improve reliability, it is crucial to understand the factors influencing capture and recapture probabilities. Monitoring designs based on this knowledge can help increase capture and recapture probabilities.

Low detectability can be caused by, for example, species-specific traits (e.g., camouflage and behavior), individual traits (e.g., age and sex), survey-specific factors (e.g., field effort and observer experience), weather conditions, and site-specific factors (e.g., vegetation structure) (Mazerolle et al. 2007; Dénes et al. 2015). Every factor that could influence detectability cannot be considered, particularly if synergistic or subtle effects exist that are beyond researcher control. However, to minimize effects of low detectability and conduct the study during optimal conditions (i.e., when detection rate is highest), it is essential to test the impact of a range of factors.

Assessing the effort required to reach a certain level of precision on parameter estimates is crucial for implementing efficient monitoring schemes or obtaining a sufficient statistical power to test specific hypotheses (e.g., on population trends). Such analyses are usually conducted through simulations relying on some a priori knowledge or assumptions of the population sizes and capture and recapture probabilities, which may be obtained from a pilot study or expert knowledge. However, only a few studies have simulated field effort in a capture–recapture context (e.g., Al-Chokhachy et al. 2009; Lieury et al. 2017), particularly for species with low detection rates (e.g., Gerber et al. 2014; Peel et al. 2015).

Optimization of capture–recapture protocols is especially important for elusive species with short life spans or variable activity patterns, conditions that may significantly hamper monitoring. These characteristics are particularly common in invertebrates and many amphibians, reptiles, and small mammals. The Crau plain grasshopper (*Prionotropis rhodanica*) is useful for testing how monitoring schemes for elusive species with a short activity period can be optimized. This grasshopper is perfectly camouflaged, resembling stones typical of its habitat, and remains mostly immobile and silent (Supporting Information). Monitoring the species' population size and trend is also challenging because of its short adult period. Nymphs of this univoltine species hatch in early April and pass 5 instars before reach adulthood at the end of May. The adult phase lasts <40 days (Foucart 1995), restricting the available period for capture–recapture studies on mature individuals.

We used data from 5 capture–recapture studies conducted on the species to test which methodological and environmental factors affect capture and recapture probabilities and the precision of estimates of population size. We hypothesized that field effort, season, and weather conditions have strong effects on capture and recapture probabilities and that the precision of estimates of population size is improved considerably by incorporating these factors in capture–recapture models. Based on the estimates of the capture–recapture analysis, we conducted a simulation study to examine the precision of estimation of population size in response to varying capture and recapture probabilities and number of sampling occasion to identify the minimum number of sampling occasions required to obtain unbiased estimates of population size. Based on the results of the estimates and the simulation study, we conducted 2 optimized capture–recapture studies and compared the precision of estimates of population size with those of previous years. We hypothesized that estimates of population size from the optimized design (i.e., fewer sampling occasions) are more precise than those from previous studies that were longer and had higher sampling effort. Finally, we simulated scenarios to investigate to what extent estimates of population size in capture–recapture studies of elusive species are sufficiently robust to inform the application of criteria C and D of the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (IUCN 2017).

Methods

Study Species

Prionotropis rhodanica is a large grasshopper (adult females mean body size 45 mm; males 31 mm [Foucart 1995]). Both sexes are flightless and their mobility is low (maximum dispersal distance of 50 m during adult phase) (Foucart & Lecoq 1996). This habitat specialist is endemic to the Crau steppe, a Mediterranean stone steppe in southern France. The species was formerly widely distributed in the entire steppe (former extent approximately 50,000 ha) but has lost large parts of its habitat to expansion of industrial and agricultural areas (Foucart & Lecoq 1998). Less than 10,000 ha of habitat remain (Tatin et al. 2013); 7,400 ha are protected. The species is listed as critically endangered on the IUCN Red List (Hochkirch & Tatin 2016), and intensive grazing is a major threat (Piry et al. 2018; Bröder et al. 2019). Only 3 spatially separated subpopulations remain (Hochkirch & Tatin 2016). A conservation strategy was compiled for the species in 2014 (Hochkirch et al. 2014). One objective was the development of a monitoring scheme to survey ongoing population trends and the species' response to conservation action.

Study Sites

We studied the 3 remaining subpopulations of *P. rhodanica* (labeled according to the location): Calissane, BMW, and Peau de Meau. Calissane has the largest population located mainly inside the reserve (except for 40 ha on military property). The BMW is private and surrounded by a high wall. Habitat in BMW is limited (around 150 ha), and the grasshopper occurs inside proving grounds for cars in 2 areas. Only 1 of these area was used for this study because of limited access to the other area. The subpopulation Peau de Meau is the only remaining in the center of the Crau and is located entirely inside the reserve. The spatial extent of the subpopulation is small (approximately 9 ha), and it is a remnant of a formerly large subpopulation (Hochkirch et al. 2014). The populated

Table 1. Comparison of the capture-recapture studies for the Crau Plain grasshopper subpopulations Calissane, Peau de Meau, and BMW and estimates of their population size.[a].

	Not optimized					*Optimized*	
	Calissane		*Peau de Meau*		*BMW*	*Calissane*	*Peau de Meau*
Study feature	*2013*	*2017*	*2015*	*2017*	*2016*	*2018*	*2019*
Study area (ha)	9	9	7	7	7.5	9	7
Study period	3 June – 5 July	29 May – 30 June	1 June – 10 July	26 May – 30 June	3 June – 11 July	11 June – 4 July	3 June – 25 June
First adults of the season	3 June	20 May	29 May	20 May	2 June	31 May	25 May
Total occasion number	24 (12)[b]	20	28	19	17	16	16
Occasions with captures	22 (12)[b]	18	19	17	13	16	16
Occasions without captures	2 (0)[b]	2	9	2	4	0	0
Marked individuals	177	65	32	60	32	171	189
No. of recaptures (%)	11 (6.2)	3 (4.6)	7 (21.9)	8 (13.3)	0 (0)	10 (5.8)	65 (29.6)
Occasions in optimal period (%)	58	67	42	53	54	81	81
Occasions in extended period (%)	75	89	63	82	85	100	100
Estimates of population size (95% CI)[c]	298 (259–356)	84 (75–102)	43 (37–55)	81 (72–100)	50 (42–67)	227 (205–263)	251 (227–290)
Coefficient of variation (%)[c]	8.1	7.7	10.4	8.5	12.6	6.4	6.3

[a]*The not optimized studies were used to optimize the study design, which was applied during the studies Calissane 2018 and Peau de Meau 2019 (optimized studies).*
[b]*Morning and afternoon occasions were pooled to a single occasion for data analyses.*
[c]*Results from analyses combining all studies (2013–2019) and the model including phenology as covariate.*

area of Peau de Meau is fenced when the grasshopper is present (April to early July) to avoid negative effects from sheep grazing.

Capture–Recapture Study

Capture–recapture was performed similarly for the 3 subpopulations in 4 different years (2013, 2015, 2016, and 2017). In 2018 and 2019 an optimized protocol was tested in the subpopulations Calissane and Peau de Meau (Table 1). Because the survey method was time-consuming and requires 3 observers per site, we could not study >1–2 subpopulations each year. All studies were conducted during the adult phase because we aimed to estimate the number of mature individuals. Furthermore, nymphs would lose their marks during molt (Besnard et al. 2007).

Three observers walked at a distance of approximately 1 m to each other across the entire study area for 3 h. The direction was changed when randomly called for by 1 of the 3 observers. For the study in Calissane in 2013, sampling was conducted in the morning and afternoon (total survey time 6 h). These 2 occasions were later pooled into a single occasion to reduce 0s in the capture history. Each individual was captured and marked by writing a number on the pronotum with a permanent paint marker (Edding 780), which does not harm grasshoppers (Laußmann 1994). Location of capture was recorded, and individuals were released where they were captured.

Testing Covariate Effects and Estimating Population Sizes and Capture Probabilities

Data from the capture–recapture studies of 2013–2017 were used for testing effects of covariates on capture and recapture probabilities and estimates of population size. These results were used to optimize the protocol for 2018 and 2019. The very low number of recaptures precluded the fit of open population models, so we ran closed population models, which require a lower number of parameters. We assumed that closure (i.e., no emigration, immigration, birth, or mortality) is mostly true because the species has a very low mobility and because sampling occasions were conducted over only about 1 month during the adult phase, which is <40 days. We applied a closed capture–recapture modeling procedure (Otis et al. 1978) in Mark 6.2 (White & Burnham 1999) and combined capture histories of all studies in a single data set. The simultaneous modeling of all data allowed sharing of capture parameters among studies, which provides higher precision of estimates of population sizes. It also allows population size modeling for a study without recaptures (BMW 2016). Because all parameters were shared among data sets, parameter numbers were small (most models had 8 parameters), which is essential for sparse data to prevent overparametrization. We defined groups based on the subpopulation and year of study (i.e., Calissane 2013, Calissane 2017, Peau de Meau 2015, etc.), which allowed estimation of population size for each single group. Because of the different number of sampling occasions in each study (12–19 occasions

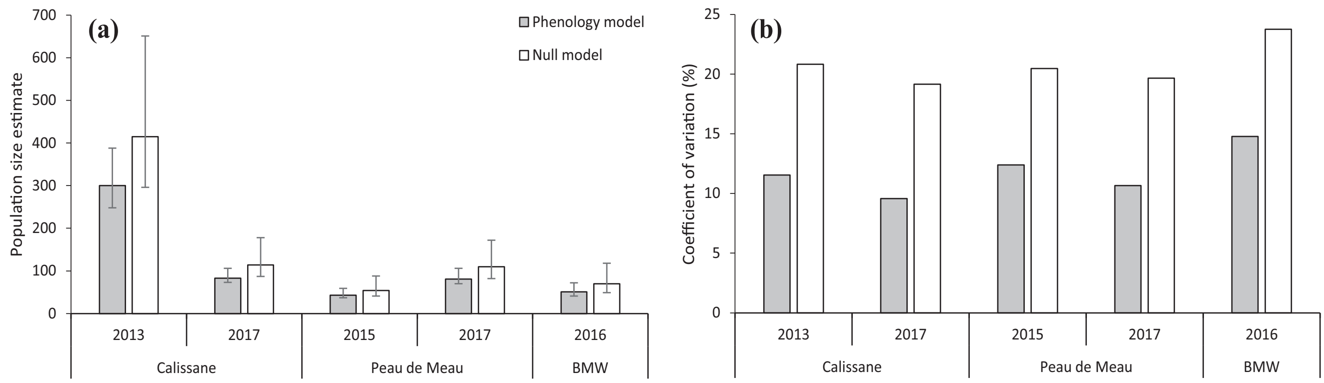

Figure 1. Comparison of the model including phenology (i.e., number of days since first detection of adults in a year) as covariate (phenology model) and the model without covariate (null model) for the 5 capture–recapture studies from 2013 to 2017: (a) estimates of population size and 95% CI and (b) coefficient of variation.

[Table 1]) zeros were added to some sites to get the same number of occasions for all sites in the combined data set. Their corresponding parameters (capture and recapture rates) were later fixed to zero.

The low recapture rate made it necessary to run simple models with few parameters. Hence, we applied constant models with no temporal variation and no group differences and assumed either equal encounter probabilities (capture probability [p] = recapture probability [c]) or implied difference ($p \neq c$). Both models were ranked based on the corrected Akaike's information criterion (AIC_c). Delta AIC_c between both models was 6.2, and the model with different capture and recapture probabilities was ranked first (Supporting Information). This model (7 parameters, $p = 0.05$ [95% CI: 0.03–0.08], $c = 0.01$ [0.007–0.015]) (estimates of population size in Fig. 1) was used as a basis for testing the effects of covariates (e.g., temperature, date, and field effort [Supporting Information]) on capture and recapture probabilities.

All covariates were scaled and centered for standardization, and we explored whether their relationship with capture and recapture probabilities was linear or quadratic (Supporting Information). For identifying which covariate explained most variation in capture and recapture probabilities, we fitted models that include 1 covariate (i.e., either linear or quadratic model of each covariate) and compared the AIC_c of these models and the null model (i.e., model without a covariate). Confidence intervals of the estimates of population size of these models were neither huge nor very small, suggesting no overparametrization (Supporting Information). Covariate effects were further assessed by calculating the proportional reduction of deviance (D_{reduced}) as follows:

$$D_{\mathrm{reduced}} = \frac{D_{\mathrm{null}} - D_{\mathrm{covariate}}}{D_{\mathrm{null}}} \times 100, \qquad (1)$$

where D_{null} is the deviance of the null model and $D_{\mathrm{covariate}}$ is the deviance of the model including the covariate.

The coefficient of variation (CV) of estimates of population size was calculated for comparisons of the precision of the null model and the covariate model estimates. Capture and recapture probabilities and estimates of population size were retrieved for each model.

Assessing Precision of Estimates of Population Size with Simulations

To optimize the capture–recapture protocol, we aimed to identify a minimum number of occasions required to obtain reliable estimates of population size. Therefore, we simulated virtual capture–recapture data sets based on the previous estimates (i.e., population sizes of 43–300, mean capture probability of 0.07, and recapture probabilities <0.02) by testing scenarios with 10–20 sampling occasions; population sizes of 50, 100, 200, and 300; capture probabilities of $p = 0.06$, 0.07, and 0.08; and recapture probabilities of 0.01 and 0.02. We ran 1,000 simulations for each scenario with a threshold of 30% CV for estimates of population size as a minimum requirement.

We also tested scenarios with a wider range of population sizes (50, 250, 1,000, 2,500, and 10,000), capture and recapture probabilities (0.04, 0.07, 0.10, and 0.20), and numbers of sampling occasions (10, 20, and 30) to provide more general information on the application of capture–recapture for elusive species. Population sizes reflected thresholds of criteria C and D of the IUCN Red List (IUCN 2017). To provide a general simulation setup, capture and recapture probabilities were identical in all scenarios.

We simulated capture histories in R (R Core Team 2018), and models were fitted using RMark v2.2.5 (Laake 2013).

Optimization and Test of Optimized Study Design

An optimized capture–recapture design was developed based on capture and recapture probabilities and simulated scenarios describe above. The optimal number of occasions was $\geq$16. Phenology (i.e., number of days since first detection of adults in a year) correlated the most with capture and recapture rates. Consequently, we used capture probability estimates of this covariate model to optimize the study period by including only the period with above-average capture probabilities (>7% [Supporting Information]). The optimized period started 13 days after detection of first adults and lasted 20 days. To avoid habitat disturbance caused by too frequent visits, field work was extended by adding occasions with capture probabilities >5%. The period including this extended period started at day 10 of adult presence and lasted 27 days (Supporting Information).

The optimized protocol was applied in Calissane (2018) and Peau de Meau (2019). For both studies, 13 of 16 occasions (81%) were performed during the optimal period (capture probabilities $\geq$7%), and all occasions were included in the extended period (Table 1). Capture histories were added to the combined data set and population sizes were estimated using the model including phenology as covariate. The CVs of estimates of population size were used to compare the precision of the optimized studies (2018 and 2019) with the nonoptimized studies (2013 to 2017). For assessing the overlap of the nonoptimized studies with the optimized design, we calculated the percentage of occasions included in the optimized study period. We also compared the number of occasions without captures.

Results

Capture–Recapture and Estimates of Population Size

The maximum number of individuals caught during the capture–recapture studies was 254 individuals (189 captures and 65 recaptures) during the optimized study Peau de Meau 2019. In the nonoptimized studies Peau de Meau 2015 and BMW 2016, there were 32 captures and 7 recaptures and 32 captures and 0 recaptures, respectively (Table 1). Peau de Meau 2015 was the smallest subpopulation, followed by BMW 2016, and the estimates for Peau de Meau 2017 and Calissane 2017 were similar; Calissane 2013 was estimated as the largest subpopulation (Table 1; Fig. 1; Supporting Information).

Covariate Test

The model including the quadratic covariate phenology had the best AIC_c rank and the highest explained deviance (15.6%) (Supporting Information). The covariate model including date (day count started with the earliest sampling occasion of all study years) had an explained deviance of 4.1%. All other explained deviances were $\leq$3.0%. Precision of estimates of population size, in terms of 95% CIs and CVs, was considerably improved by including phenology (Fig. 1). Capture and recapture probabilities varied during the adult phase (Supporting Information); maximum capture probability was 0.10 (SE 0.02) estimated for the period from day 21 to 24 of the adult phase. The mean capture and recapture probabilities of the phenology model were, based on the estimates of all occasions, roughly estimated as 0.07 (0.03) and 0.01 (0.04). Capture probabilities above average were found from day 13 to 32 (20 days total). From day 10 to 36 of the adult phase (27 days), there were sampling occasions that had capture probabilities of at least 5%.

Required Field Effort

Estimates of population size with CVs < 30% were achieved from 11 to 17 occasions (depending on capture and recapture probabilities) for scenarios with a true population size of 300 and from 15 to 17 occasions for population sizes of 200 (Fig. 2; Supporting Information for all simulation results). The minimum required sampling occasions for scenarios with a population size of 100 and $p > 0.06$ ranged from 16 to 19. For a population of 50 and a capture probability of 0.08, minimum sampling occasions required was 19 or 20. The CVs were always >100% when population size was 100 and capture probability was 0.06 or when population size was 50 and a capture probability was 0.06 or 0.07.

We defined a minimum of 16 occasions, representing a rather conservative approach, because increased capture and recapture probabilities (i.e., $p > 0.07$ and $c = 0.02$) were assumed to be due to optimization and because reliable estimates were achieved by lower occasion numbers in scenarios with such capture and recapture probabilities and populations >100.

Optimized Studies

Studies with the optimized protocol (Calissane 2018 and 2019) had the lowest CV and no occasions without captures (Table 1). The BMW 2016 had the highest CV. Calissane 2017 was the nonoptimized study with the lowest CV and highest overlap with the optimized design (67% in optimal period and 89% in extended period). The study with the lowest overlap was Peau de Meau (2015); 42% of occasions in the optimal and 63% in the extended period overlapped. This study had the highest number of occasions without captures (9 of 28 [32%]).

Simulations of Capture–Recapture Studies for Elusive Species

All CIs included the true values of the simulated scenarios, and all median estimates of population size were equal or very close to the true value. No considerable under- or overestimation occurred, even for very small populations with extremely low capture and recapture proba-

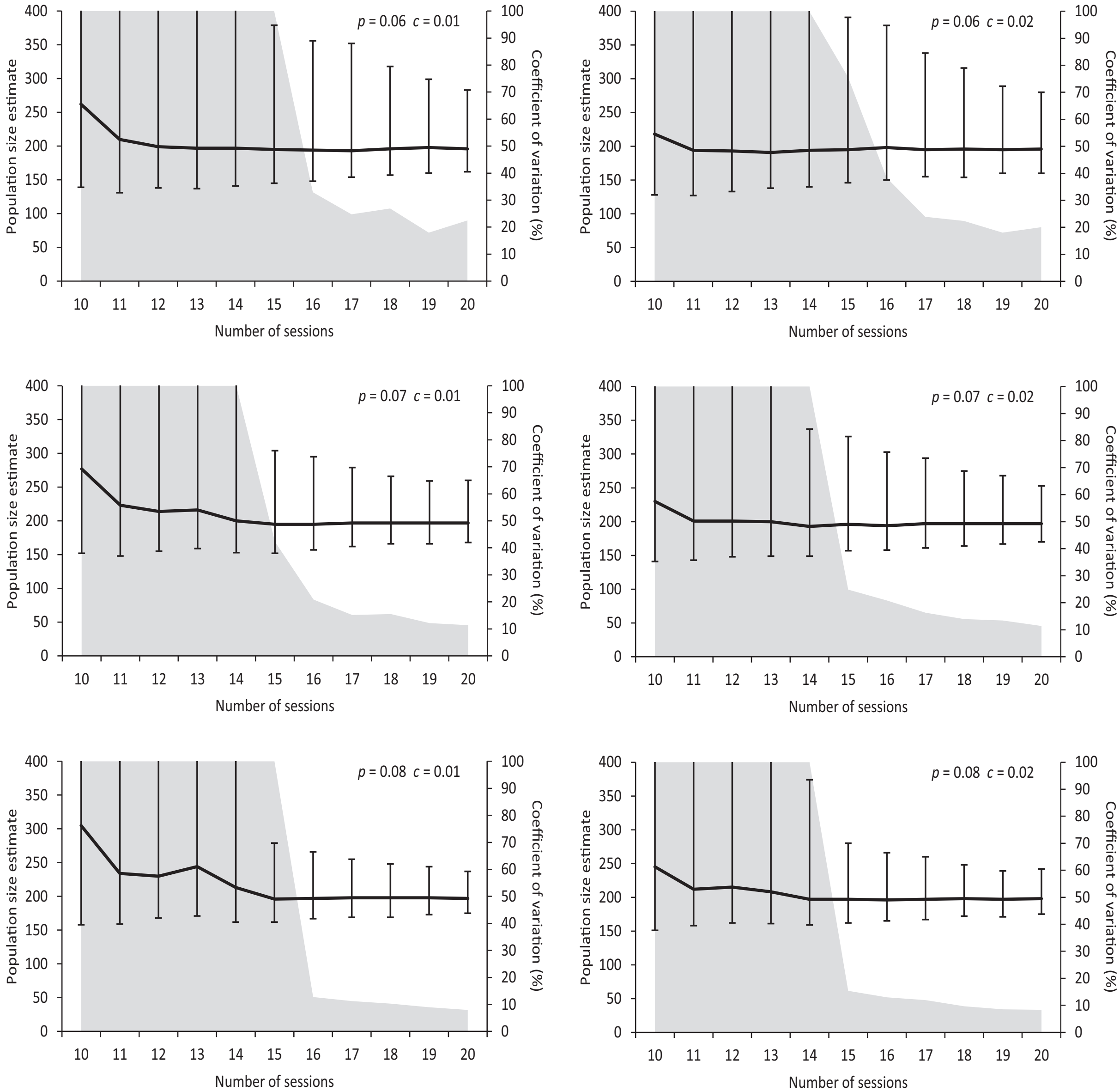

*Figure 2. Estimates of population size for the simulation scenarios based on a true population size of 200, capture probabilities (*p*) of 0.06, 0.07, and 0.08, recapture probabilities of (*c*) 0.01 and 0.02, and sampling occasion numbers from 10 to 20 (line, median; error bar, 95% CI; shaded area, coefficient of variation).*

bilities and few sampling occasions (Table 2). Most of the scenarios had small CIs and CVs <10%. Unreliable estimates with huge CIs and CVs >30% occurred only for very small populations (50 individuals) and capture and recapture probabilities of 0.04 and 0.07, respectively, when field effort was low (10 occasions).

Discussion

Our study illustrates the utility of combining empirical results of a field study with simulations for optimizing capture–recapture studies for elusive species. We found that considering environmental and methodological factors is crucial to define optimal study conditions (i.e., conditions with high capture and recapture rates) to increase precision of estimates of population size. Based on the capture–recapture estimates, we were further able to determine minimum required field effort to obtain reliable estimates by performing simulations. Our 2-step approach is generally applicable to all elusive species with short or variable activity patterns (not necessarily short-lived). Phenology is likely to be a relevant factor for many species, for example, the mating season of amphibians (Petitot et al. 2014) or the adult emergence of holometabolous insects. Moreover, meteorological

Table 2. Estimates of population size (95% CI) and coefficients of variation (CV) of simulated scenarios with different population sizes, capture and recapture probabilities, and number of sampling occasions.

		Estimates			*CV*		
		sampling occasions			*sampling occasions*		
n[a]	*p/c*[b]	*10*	*20*	*30*	*10*	*20*	*30*
50	0.04	50 (22–585,199)	50 (33–84)	50 (38–66)	3,162	26	14
50	0.07	50 (31–91)	50 (40–61)	50 (44–56)	41	11	6
50	0.10	50 (36–69)	49 (44–56)	50 (46–52)	17	6	3
50	0.20	49 (44–55)	50 (48–50)	50 (49–50)	6	2	0
250	0.04	251 (172–409)	249 (205–309)	250 (222–283)	24	10	6
250	0.07	251 (203–322)	249 (228–274)	250 (237–263)	12	5	3
250	0.10	249 (216–290)	250 (237–263)	250 (242–257)	7	3	1
250	0.20	250 (237–262)	250 (246–253)	250 (249–250)	3	1	0
1,000	0.04	1,001 (824–1,233)	1,000 (911–1,106)	1,000 (946–1,061)	11	5	4
1,000	0.07	996 (898–1,117)	999 (949–1,047)	999 (974–1,027)	6	2	1
1,000	0.10	1,000 (934–1,072)	1,000 (971–1,029)	1,000 (985–1,013)	4	1	1
1,000	0.20	999 (975–1,023)	1,000 (992–1,006)	1,000 (997–1,001)	1	0	0
2,500	0.04	2,497 (2,191–2,879)	2,503 (2,359–2,661)	2,502 (2,412–2,587)	7	3	2
2,500	0.07	2,498 (2,339–2,677)	2,497 (2,430–2,570)	2,500 (2,458–2,540)	4	1	1
2,500	0.10	2,500 (2,390–2,615)	2,498 (2,456–2,542)	2,500 (2,478–2,520)	2	1	0
2,500	0.20	2,499 (2,462–2,538)	2,500 (2,487–2,510)	2,500 (2,496–2,503)	1	0	0
10,000	0.04	10,014 (9,364–10,683)	9,987 (5,651–10,236)	9,994 (9,814–10,185)	3	8	1
10,000	0.07	9,997 (9,678–10,348)	10,001 (9,852–10,147)	10,001 (9,915–10,080)	2	1	0
10,000	0.10	9,994 (9,790–10,245)	9,979 (9,907–10,084)	10,001 (9,955–10,043)	1	0	0
10,000	0.20	9,999 (9,918–10,080)	9,999 (9,977–10,021)	9,997 (9,982–10,006)	0	0	0

[a]*Simulated population size.*
[b]*Simulated capture (p) and recapture probability (c).*

factors determine seasonal or daily activity patterns (e.g., reptiles [Christy et al. 2010], rodents [Paise & Vieira 2006], beetles [Roets et al. 2013], and slugs [Reich et al. 2017]). We recommend systematically recording potential covariates that may affect detection probability of elusive species. Simulation studies based on empirical information could further minimize field effort. The R code provided allows adapting the simulation procedure to specific objectives within the framework of closed population modeling (Supporting Information).

Optimization of Capture–Recapture Design

Identifying the major parameters affecting capture and recapture probabilities and adapting protocols to conditions with high capture and recapture rates was key in the optimization process. In our model species, phenology (i.e., days since first detection of adults) was the main parameter affecting capture and recapture probabilities. The emergence of adults varied among years (Table 1), explaining why date had little explanatory power. Variation in phenology in response to environmental conditions is a common phenomenon in many invertebrates and even in vertebrates (Rudolf 2019). Lack of knowledge about such seasonal effects may result in collection of inappropriate data, which is particularly problematic if they are used to make conservation decisions (Samways & Grant 2007). At first glance, using phenology information to initiate fieldwork appears complicated compared with date because presence of adults needs to be confirmed first. Yet, in our model species, adult appearance is recorded on a regular basis as a byproduct of other conservation activities. Moreover, directed searches at known density hotspots may help obtain the information with little additional fieldwork. Contrary to our initial assumptions temperature, wind speed, and study effort did not influence capture and recapture probabilities, all of which may be important for other elusive species (e.g., Schulte et al. 2013). The lack of effects of daily survey effort may be explained by a decrease in observer attention through time.

Including methodological and environmental variables in capture–recapture modeling is not only helpful in understanding relationships between variables and model parameters, but also in increasing precision of parameter estimates (Pollock 2002). In our study, estimates of population size were notably more precise in models including covariates than in the null model. The addition of covariates also provided precise estimates of capture and recapture probabilities and information on their variation throughout the season, which allowed us to optimize the capture–recapture design. The results of the 2 studies conducted with this optimized design confirmed the efficacy of the procedure because estimates of population size became substantially more precise despite much lower study effort (−6% to −27% sampling occasions). Moreover, the optimized studies were the only studies without occasions with no grasshopper detections, increasing the motivation of the field team, a factor that may also influence capture probabilities.

Capture–Recapture Modeling for Elusive Species

One common attribute of capture–recapture studies on elusive species is sparse data sets, even when field effort and population sizes are large. Such data sets frequently lead to convergence or parameter identifiability issues during modeling. One basic but efficient option to improve inference in such contexts relies on the combination of data sets (capture histories) collected over several sites or years (White 2005). This approach allows sharing capture parameters among data sets and has, therefore, the potential to improve precision of estimates of population size even when some data sets do not include recaptures (as in our study for BMW). However, such a combination of data sets generates constraints on modeling. The most important is that when data are collected at irregular intervals (i.e., between studies or even within the same study) and when number of capture occasions and length of study period vary between years or sites, parametrization of adequate models can be challenging. In our example it was impossible to fit open population models. The heterogeneity of the field data precluded the use of constant models for open population modeling (e.g., constant entrance or survival probabilities), and few data precluded fitting more complex models. In such cases there are 2 solutions: develop highly standardized field procedures so that data sets can be naturally combined or develop a study design that fulfils the assumptions of simpler models, such as closed population ones; that is, minimize the probability of birth, death, immigration, or emigration over the sampling period. The latter can typically be achieved by collecting data over a relatively short period (Nichols 1992). In the case of *P. rhodanica*, we assumed a closed population (see Methods). Nevertheless, demographic closure cannot be completely reached because some nymphs can still molt at the beginning of the adult season and death occurs at the end of the adult season. Our optimization process helped minimize the influence of demographical changes by shortening the study period. However, mortality caused by, for example, predation and pathogens cannot be controlled and is supposed to occur to some degree during the entire study period.

Reliability of Capture–Recapture Studies for Elusive Species

Most of our simulations for estimates of population size based on the IUCN Red List criteria thresholds produced unbiased and sufficiently precise estimates—even for scenarios with relatively few sampling occasions. Only the estimate for the scenario with very low capture probability ($p = 0.04$), very small population size (50 individuals), and low field effort (10 occasions) was poor. Capture–recapture can, therefore, be considered generally applicable for elusive species and reliable enough to inform red-list assessments. If required, the IUCN Red List Guidelines (IUCN 2017) provide guidance on how to deal with uncertainties.

Poor information on population size may be more critical in the context of monitoring of population trends. In our simulations, field effort required to achieve reliable estimates was comparatively high for very small populations with very low capture probabilities. Applying capture–recapture for monitoring of such species may thus be costly. Optimizing field protocols, as illustrated in our example, is therefore important in such cases.

Management Implications

Our study provides guidance on optimizing capture–recapture designs for elusive species, based on a real-world example of a critically endangered and highly elusive grasshopper species. Performing simulations based on species-specific capture and recapture probabilities helped us improve the field protocol substantially. This universal approach is applicable to many other elusive species. Alternative methods to estimate abundance of elusive species are limited. Site occupancy seems attractive because its sampling method is less extensive. However, extracting abundance from site occupancy data (Royle & Nichols 2003) is only appropriate if detection probability is mainly influenced by species abundance (Blanc et al. 2014), which is not the case for elusive species with variable activity patterns. An N-mixture model is very sensitive to heterogeneity in abundance among sites and often associated with problems of parameter identifiability, notably if detection probability is highly variable (Couturier et al. 2013). For distance sampling, large amounts of data are typically needed, which is a critical point for elusive species, and the method is very sensitive if individuals at 0 distance from the survey point or lines are missed (Buckland et al. 2008) or if individuals are not available because of variable activity. Overall, capture–recapture is probably the most suitable method to achieve reliable abundance estimates for elusive species, but its feasibility mainly depends on the available resources. Because survey duration is a central constraint for designing cost-effective monitoring schemes (Lieury et al. 2017), knowledge of required field effort is crucial. In our example, the minimum required field effort of 16 sampling occasions is still time-consuming. Even though the total number of working hours needed (3 people $\times$ 3 h $\times$ 16 occasions = 144 h) does not appear to be too high, it needs to be invested during a short period and—if all remaining subpopulations of the species are being monitored—on 3 sites. Although capture–recapture studies on elusive species will remain difficult and costly compared with other species, our optimization procedure can help conservation practitioners and researchers improve data quality and minimize monitoring effort for elusive species.

Acknowledgments

The survey was funded by grants of the Mohamed bin Zayed Species Conservation Fund (project number 142510206), the Studienstiftung des deutschen Volkes, the EU program ERASMUS + via the German Academic Exchange Service (DAAD), the Conseil départemental des Bouches-du-Rhône, and the Direction Regionale de l'environnement de l'aménagement et du logement de Provence Alpes-Côte d'Azur. We thank the Conservatoire d'espaces naturels de Provence-Alpes-Côte d'Azur and its team for support during fieldwork and everyone else who participated in data collection, especially E. Miller, G. Coste, G. Paulus, E. Becker, Y. Toutain, T. Seibel, J. Schmitt, A. Danielczak, E. Gromelle, H. Frances, M. Rambaud, T. Vanhoutte, M. Lebail, and D. Schambach. We thank Trier University for providing equipment.

Supporting Information

Picture of adult Crau plain grasshopper (Appendix 1), list of tested covariates (Appendix 2), model ranking (Appendix 3 – Appendix 5), estimates of population size for all tested models (Appendix 6), capture probability estimates used for optimization of the study period (Appendix 7), additional simulation results (Appendix 8), and R code for simulations (Appendix 9) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

Literature Cited

Al-Chokhachy R, Budy P, Conner M. 2009. Detecting declines in the abundance of a bull trout (*Salvelinus confluentus*) population: understanding the accuracy, precision, and costs of our efforts. Canadian Journal of Fisheries and Aquatic Sciences **66:**649–658.

Besnard A, Piry S, Berthier K, Lebreton J-D, Streiff R. 2007. Modeling survival and mark loss in molting animals: recapture, dead recoveries, and exuvia recoveries. Ecology **88:**289–295.

Blanc L, Marboutin E, Gatti S, Zimmermann F, Gimenez O. 2014. Improving abundance estimation by combining capture–recapture and occupancy data: example with a large carnivore. Journal of Applied Ecology **51:**1733–1739.

Bröder L, Tatin L, Danielczak A, Seibel T, Hochkirch A. 2019. Intensive grazing as a threat in protected areas: the need for adaptive management to protect the Critically Endangered Crau plain grasshopper *Prionotropis rhodanica*. Oryx **53:**239–246.

Buckland ST, Marsden SJ, Green RE. 2008. Estimating bird abundance: making methods work. Bird Conservation International **18:**S91–S108.

Chadès I, McDonald-Madden E, McCarthy MA, Wintle B, Linkie M, Possingham HP. 2008. When to stop managing or surveying cryptic threatened species. Proceedings of the National Academy of Sciences **105:**13936–13940.

Christy MT, Yackel Adams AA, Rodda GH, Savidge JA, Tyrrell CL. 2010. Modelling detection probabilities to evaluate management and control tools for an invasive species. Journal of Applied Ecology **47:**106–113.

Couturier T, Cheylan M, Bertolero A, Astruc G, Besnard A. 2013. Estimating abundance and population trends when detection is low and highly variable: a comparison of three methods for the Hermann's tortoise. The Journal of Wildlife Management **77:**454–462.

Dénes FV, Silveira LF, Beissinger SR. 2015. Estimating abundance of unmarked animal populations: accounting for imperfect detection and other sources of zero inflation. Methods in Ecology and Evolution **6:**543–556.

Foucart A. 1995. *Prionotropis rhodanica* Uvarov, 1923 (Acridoidea, Pamphagidae, Akicerinae), acridien protégé de la Crau (Bouches-du-Rhône, France). PhD thesis. École pratique des hautes études and Cirad-gerdat-prifas, Montpellier, France.

Foucart A, Lecoq M. 1996. Biologie et dynamique de *Prionotropis hystrix rhodanica* Uvarov, 1923, dans la plaine de la Crau (France)(Orthoptera, Pamphagidae). Bulletin de la Société Entomologique de France **101:**75–87.

Foucart A, Lecoq M. 1998. Major threats to a protected grasshopper, *Prionotropis hystrix rhodanica* (Orthoptera, Pamphagidae, Akicerinae), endemic to southern France. Journal of Insect Conservation **2:**187–193.

Gerber BD, Ivan JS, Burnham KP. 2014. Estimating the abundance of rare and elusive carnivores from photographic-sampling data when the population size is very small. Population Ecology **56:** 463–470.

Hochkirch A, Tatin L. 2016. *Prionotropis rhodanica*. The IUCN red list of threatened species. Available from http://doi.org/10.2305/IUCN.UK.2016-3.RLTS.T15038481A47713628.en (accessed October 2018).

Hochkirch A, Tatin L, Stanley Price M. 2014. Crau plain grasshopper, a strategy for its conservation. IUCN-SSC & CEN-PACA, Saint-Martin-de-Crau, France.

IUCN (International Union for Conservation of Nature). 2017. Guidelines for using the IUCN red list categories and criteria. Version 13. IUCN, Gland, Switzerland. Available from http://www.iucnredlist.org/documents/RedListGuidelines.pdf (accessed January 2019).

Laake JL. 2013. RMark: an R interface for analysis of capture-recapture data with MARK. Processed report 2013-01. Alaska Fisheries Science Center, National Marine Fisheries Service, Seattle, Washington.

Laußmann H. 1994. Werden Feldheuschrecken durch die Markierung mit Lackmalstiften in ihrer Vitalität beeinträchtigt? Articulata **9:** 37–41.

Lieury N, Devillard S, Besnard A, Gimenez O, Hameau O, Ponchon C, Millon A. 2017. Designing cost-effective capture-recapture surveys for improving the monitoring of survival in bird populations. Biological Conservation **214:**233–241.

Mazerolle MJ, Bailey LL, Kendall WL, Andrew Royle J, Converse SJ, Nichols JD. 2007. Making great leaps forward: accounting for detectability in herpetological field studies. Journal of Herpetology **41:**672–689.

Nichols JD. 1992. Capture-recapture models. Using marked animals to study population dynamics. BioScience **42:**94–102.

Otis DL, Burnham KP, White GC, Anderson DR. 1978. Statistical inference from capture data on closed animal populations. Wildlife Monographs **62:**3–135.

Paise G, Vieira EM. 2006. Daily activity of a neotropical rodent (*Oxymycterus nasutus*): seasonal changes and influence of environmental factors. Journal of Mammalogy **87:**733–739.

Peel D, Bravington M, Kelly N, Double MC. 2015. Designing an effective mark–recapture study of Antarctic blue whales. Ecological Applications **25:**1003–1015.

Petitot M, Manceau N, Geniez P, Besnard A. 2014. Optimizing occupancy surveys by maximizing detection probability: application to amphibian monitoring in the Mediterranean region. Ecology and Evolution **4:**3538–3549.

Piry S, Berthier K, Streiff R, Cros-Arteil S, Tatin L, Foucart A, Bröder L, Hochkirch A, Chapuis M-P. 2018. Fine-scale interactions between habitat quality and genetic variation suggest an impact of grazing on the critically endangered Crau Plain grasshopper (Pamphagidae: *Prionotropis rhodanica*). Journal of Orthoptera Research **27:** 61–73.

Pollock KH. 2000. Capture-recapture models. Journal of the American Statistical Association **95:**293–296.

Pollock KH. 2002. The use of auxiliary variables in capture-recapture modelling: an overview. Journal of Applied Statistics **29:** 85–102.

R Core Team. 2018. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from https://www.R-project.org/ (accessed February 2018).

Reich I, Mc Donnell R, Mc Inerney C, Callanan S, Gormally M. 2017. EU-protected slug *Geomalacus maculosus* and sympatric *Lehmannia marginata* in conifer plantations: What does mark-recapture method reveal about population densities? Journal of Molluscan Studies **83:**27–35.

Roets F, Pryke JS, McGeoch MA. 2013. Abiotic variables dictate the best monitoring times for the endangered Table Mountain stag beetle (*Colophon westwoodi* Gray 1832, Coleoptera: Lucanidae). Journal of Insect Conservation **17:**279–285.

Royle JA, Nichols JD. 2003. Estimating abundance from repeated presence–absence data or point counts. Ecology **84:**777–790.

Rudolf VHW. 2019. The role of seasonal timing and phenological shifts for species coexistence. Ecology Letters **22:**1324–1338.

Samways MJ, Grant PBC. 2007. Honing Red List assessments of lesser-known taxa in biodiversity hotspots. Biodiversity and Conservation **16:**2575–2586.

Schulte U, Hochkirch A, Wagner N, Jacoby P. 2013. Witterungsbedingte Antreffwahrscheinlichkeit der Schlingnatter (*Coronella austriaca*). Zeitschrift für Feldherpetologie **20:**197–209.

Specht HM, Reich HT, Iannarilli F, Edwards MR, Stapleton SP, Weegman MD, Johnson MK, Yohannes BJ, Arnold TW. 2017. Occupancy surveys with conditional replicates. An alternative sampling design for rare species. Methods in Ecology & Evolution **8:**1725–1734.

Sutherland WJ, Pullin AS, Dolman PM, Knight TM. 2004. The need for evidence-based conservation. Trends in Ecology & Evolution **19:**305–308.

Tatin L, Wolff A, Boutin J, Colliot E, Dutoit T. 2013. Ecologie et conservation d'une steppe méditerranéenne: la plaine de Crau. Editions Quae, Verseilles.

Thompson W. 2004. Sampling rare or elusive species. Concepts, designs, and techniques for estimating population parameters. Island Press, Washington, D.C.

White GC. 1982. Capture-recapture and removal methods for sampling closed populations. Los Alamos National Laboratory, Los Alamos, New Mexico.

White GC. 2005. Correcting wildlife counts using detection probabilities. Wildlife Research **32:**211–216.

White GC, Burnham KP. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study **46:**120–139.

Willson JD, Winne CT, Todd BD. 2011. Ecological and methodological factors affecting detectability and population estimation in elusive species. The Journal of Wildlife Management **75:**36–45.

Yoccoz NG, Nichols JD, Boulinier T. 2001. Monitoring of biological diversity in space and time. Trends in Ecology & Evolution **16:**446–453.