Make flying-fox hunting sustainable again: Comparing expected demographic effectiveness and hunters' acceptance of more restrictive regulations

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Abstract Hunting is a major threat to many species of wildlife. However, managing hunting systems to ensure their sustainability requires a thorough demographic knowledge about the impact of hunting. Here we develop a framework integrating ecological, modelling and sociological data to achieve a sustainability assessment of flying-fox hunting in New Caledonia and assess the relative merits of alternative management policies. Using age-specific stochastic population models, we found that the current annual hunting rate [5.5−8.5%] is likely to lead to a severe decline (− 79%) of *Pteropus* populations over the next 30 years. However, a majority of hunters surveyed (60%) were willing to soften their practices, offering an opportunity for adaptive management. Recurrent temporary hunting ban (at least 1 year out of 2) in combination with protected areas (≥ 25%) appears as the most effective and most accepted management option. Our integrative approach appears to be a promising method for ensuring that traditional hunting systems can remain sustainable in a rapidly changing world.

Keywords Adaptive management · Flying-fox · Harvest sustainability · Hunters' survey · Population viability analysis · Pteropus

INTRODUCTION

The harvesting of wildlife, particularly by hunting, is one of the main drivers of the current loss of biodiversity worldwide (Ceballos et al. 2017; Ripple et al. 2019). Hunting can interfere with genetic, demographic and evolutionary processes and make wild populations collapse when excessive (Coltman et al. 2003; Milner-Gulland et al. 2003; Sandercock et al. 2011). Widespread transformation of hunting motivations from subsistence to recreational and commercial use, increasing human populations, improved hunting technologies and facilities for large-scale trading are increasing pressure on exploited populations (Milner-Gulland and Bennett 2003; Fa et al. 2005; Ripple et al. 2016; Benítez-López et al. 2017).

Management aimed at ensuring the sustainability of hunted species is therefore crucially needed and relies on the knowledge of their population dynamics to assess the relative effectiveness of alternative management strategies (Sutherland 2001; Nichols and Williams 2006). However, wildlife management authorities typically face challenges in obtaining population and harvest data that will ultimately support population models, making it difficult to assess hunting sustainability (Milner-Gulland et al. 2008; Weinbaum et al. 2013; Johnson et al. 2018). In addition, data on the compliance and acceptability of current or future regulations by hunters are often lacking. However, assessing the level of regulation acceptance by hunters is a crucial step in designing an adaptive management approach based on ensuring the adoption of efficient new regulations capable of improving population dynamics of hunted species (Rowcliffe et al. 2004; Nichols and Williams 2006; Schroeder et al. 2014).

Mammals are popular game species worldwide, with at least 1228 of the 5899 species (21%) hunted for consumption or other use (Bowyer et al. 2019; IUCN 2020). According to the IUCN Red List (2020), hunting represents a threat for 47% of the 1654 threatened mammalian species (CR, EN, VU & NT), some groups being more threatened and/or hunted than others. The ecologically and

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taxonomically diverse Order Chiroptera represents a group of ca. 1400 species of bats among which more than a quarter are threatened (Frick et al. 2020; IUCN 2020). Its Genus *Pteropus,* relatively large fruit-eating species popularly known as flying-foxes, is facing a global decline, with 41 of its 59 extant species listed as Threatened and four species were recently designated extinct, making this one of the most endangered genera of mammals (IUCN 2020). Fifty-three *Pteropus* are endemic or restricted to islands, which increases their vulnerability (Vincenot et al. 2017). Finally, 51 flying-fox species are hunted for subsistence, recreational and cultural purposes with some species playing a central role in traditional Melanesian cultures (Bräutigam and Elmqvist 1990; Lavery and Fasi 2019; IUCN 2020). Research has highlighted the low resilience of large-bodied bats to hunting (Graham 1992; Brooke and Tschapka 2002; Epstein et al. 2009; Brook et al. 2019). However, the sustainability of bat hunting remains to be properly assessed so adaptive management strategies can be proposed (Berthinussen et al. 2020).

Here we investigated the sustainability of a hunting system involving two species of flying-foxes hunted in New Caledonia, South Pacific. We conducted a thorough assessment of the hunting system by gathering multiples sources of data including (1) a roost survey and fly-out counts to estimate flying-fox population size; (2) an anonymous questionnaire on hunting practices combined with hunting permit statistics to derive hunting bags; (3) roost monitoring to estimate fecundity; and (4) age-at-death data from flying-foxes killed by hunting to estimate adult survival rate and age-specific susceptibility to hunting. Crucially, the questionnaire also evaluated hunters' willingness to accept alternative regulations aiming at moving towards sustainability. Finally, we built a stochastic demographic model, accounting for parameter uncertainty, to quantify the current impact of hunting on the flying-fox population and compare the expected demographic effectiveness to the level of acceptance by hunters of proposed new hunting regulations, as a first step towards adaptive management.

MATERIALS AND METHODS

Study area and species

The study took place in the mainland of New Caledonia (Northern and Southern provinces excluding Loyalty Islands; hereafter New Caledonia; Fig. 1). New Caledonia (21.3° S, 165.5 E) was colonised by Melanesians (Kanaks) ca. 3 200 years ago, joined by Polynesians and other communities following the arrival of Europeans (primarily French) in the nineteenth century. Hunting, fishing and family farming remain important sources of food for New Caledonians (Bouard et al. 2019) and hunting is of cultural importance, especially for Kanaks. Bats are the only native land mammals in the archipelago and flying-foxes and native pigeons that were once hunted only by Kanaks are now hunted for food and recreational purposes by all communities.

The endemic ornate flying-fox *Pteropus ornatus* Gray, 1870 and the more widespread native Pacific flying-fox *P. tonganus geddiei* Quoy & Gaimard, 1830, respectively, classified as Vulnerable and Least Concern (IUCN 2020), share diurnal roosts and most ecological requirements. These two large-bodied bats are difficult to distinguish during fly-out counts at dusk and are not selected by hunters. Here, we lumped the two species together. We applied the same method as Oedin et al. (2019) to estimate total population size (both species combined) for New Caledonia.

The current hunting regulations allow hunters to take a maximum of 5 flying-foxes (either *P. ornatus* or *tonganus*) per day per hunter only during the weekends of April (8–10 hunting days per year). Trade and hunting at night or directly under a roost are prohibited. Flying-foxes are hunted mainly with shotguns at dusk when leaving their diurnal roost (pass-shooting) but also illegally at night with spotlights when the bats are foraging (Oedin et al. 2019).

Questionnaire on hunting practices & regulations

We prepared a questionnaire for hunters to investigate: (1) the proportion of hunters who hunt flying-foxes; (2) annual hunting bags in various parts of New Caledonia; and (3) their willingness to accept alternative regulations (Appendix S1). We collected 624 anonymous questionnaires between January and May 2020 from permit delivery desks and online. We assessed the number of permits delivered in 2019 and evaluated the proportion of hunters without permit from the online questionnaire to estimate the total number of hunters. Global hunting bags were estimated according to a Monte Carlo procedure to account for the uncertainty in individual hunting bags and the number flying-fox hunters (Appendix S2).

The questionnaire also included a set of new supplementary hunting regulations proposed to hunters: (1) a reduction of the number of hunting days; (2) a reduction of the maximum number of flying-foxes allowed per day per hunter; (3) a temporally recurrent hunting ban at four different frequencies (from 1 year out of 4 to 2/3); (4) a long-term moratorium (a 5-year ban followed by 5 years of hunting); and (5) the establishment of protected areas where hunting would be prohibited. Hunters were allowed to select up to three different regulations but could also state that the current regulations were appropriate or that

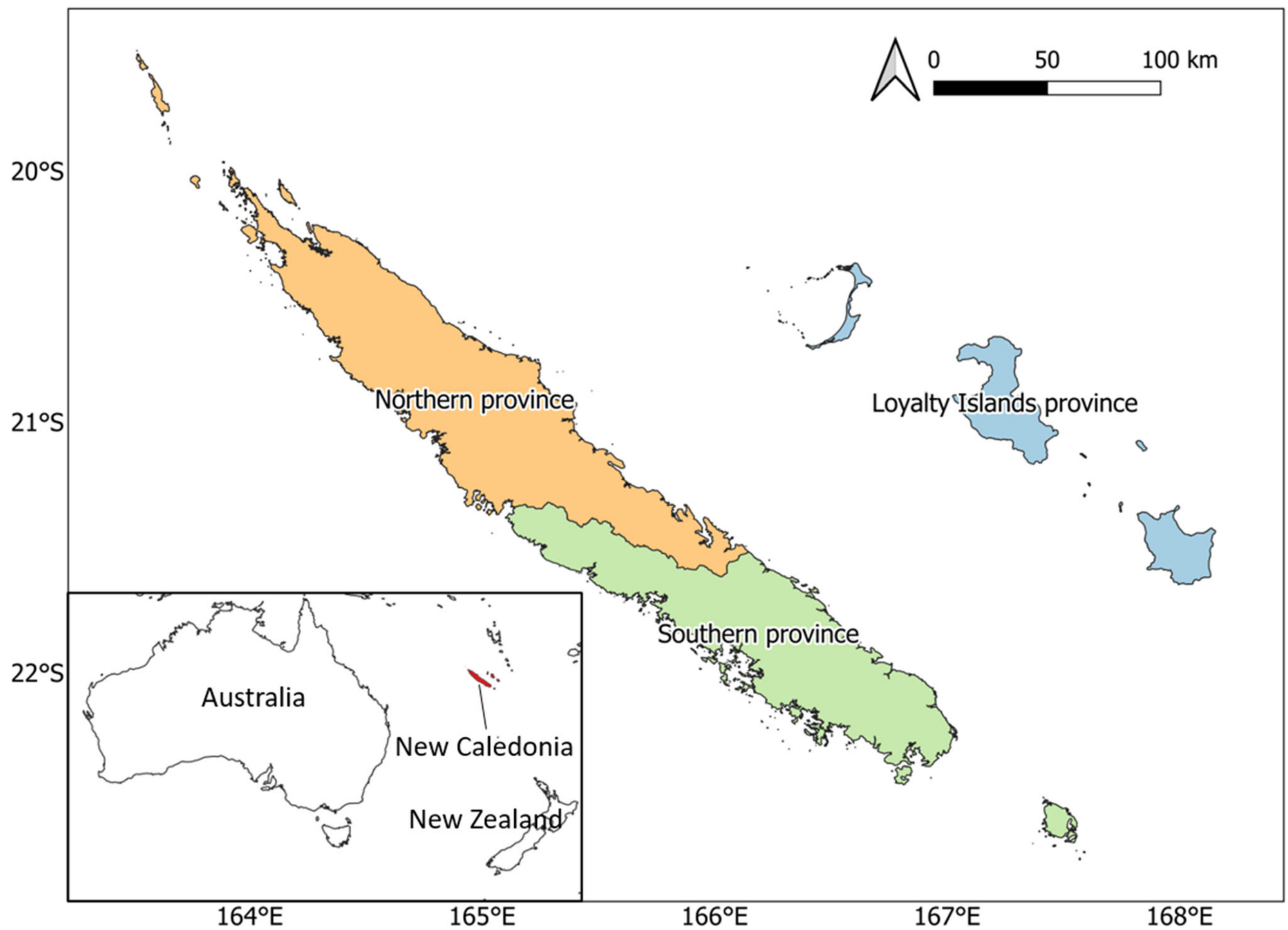

Fig. 1 Map of New Caledonia composed of three provinces: Northern, Southern and the Loyalty Islands Province, located in South Pacific (inserted map). Each province has its own hunting regulations regarding flying-fox hunting

none of the new regulations proposed were satisfactory (Appendix S1).

Estimates of flying-fox demographic rates

Data on fecundity were assessed through observations at diurnal roosts to estimate breeding success, defined as the proportion of female successfully weaning a pup (Appendix S3). Fecundity counts at seven roosts enabled 311 identifications of female reproductive status (with or without young) from 2006 to 2020. *Pteropus* females typically start breeding when 2 years old and there is evidence for maximal breeding success from 3 years old onwards (Pierson and Rainey 1992; McIlwee and Martin 2002).

We estimated age of flying-foxes hunted between 2007 and 2020 from a sample of 158 individuals (Fig. 2). Age was derived from teeth analysis (Appendix S4). We verified that the age-at-death structure did not differ significantly between the two species (χ^2_{10} = 6.33, P = 0.79) and pooled the data for estimating survival rates.

A global harvesting rate (H_g) in the study area was calculated as the ratio between the number of *Pteropus* killed each year and the total population size estimated after birth pulse (Appendix S5). Furthermore, given that young individuals are typically more sensitive to hunting than older ones, particularly for species hunted during pass-shooting (Guillemain et al. 2010; Clausen et al. 2017b), assuming a constant hunting rate through age classes might bias the impact of hunting on population dynamics. To prevent this bias, we re-distributed total hunting bags among age classes to derive age-specific hunting rates according to the age distribution observed in age-at-death data (N = 158; Fig. 2).

We estimated survival rates from a life table analysis of age-at-death data (Udevitz and Gogan 2012). We assumed a stable age structure and used a population growth rate λ = 0.99 to account for the likely decline of the flying-fox population (Oedin et al. 2019). Exponential models with variable mortality hazards were fitted to age-at-death data (Appendix S5). Because that adult survival (S_{2+}) derived from age-at-death data includes hunting-related mortality,

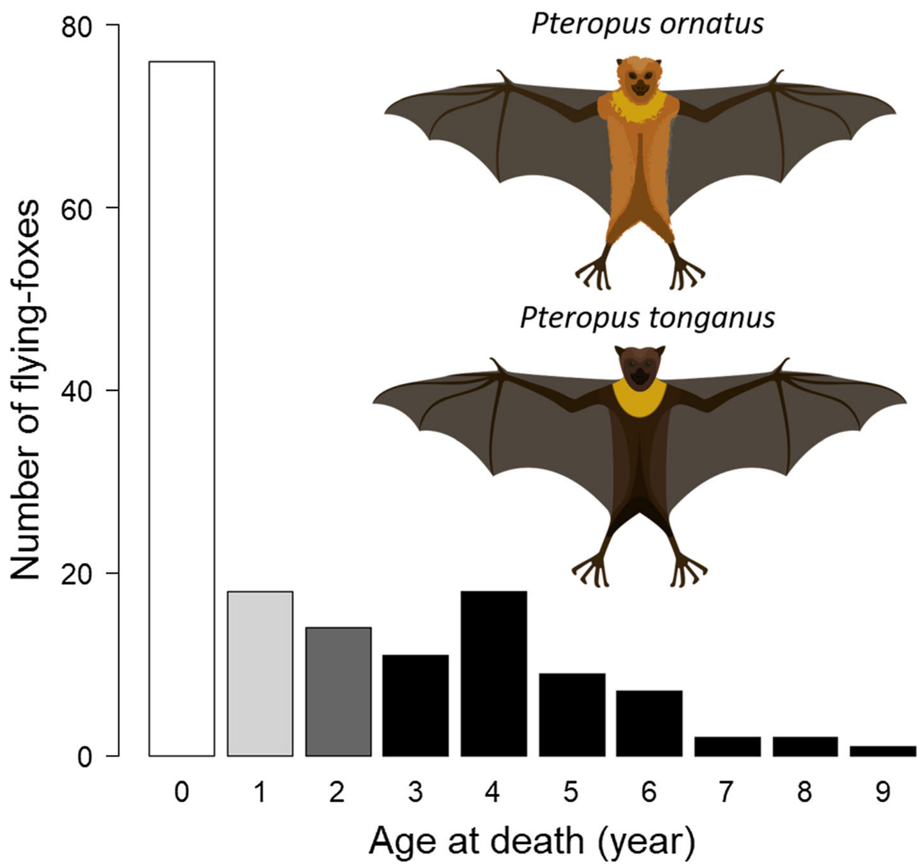

Fig. 2 The distribution of age-at-death data for 158 flying-foxes (*Pteropus ornatus* and *tonganus*) killed by hunters in New Caledonia between 2007 and 2020. The age-class '0' was not included in the survival analysis (white bar). The shade of grey indicates the different age classes used in the demographic model (age-class '1': light grey, age-class '2': dark grey, age-class '3+': black). Drawings of the two large-bodied flying-foxes in New Caledonia ©Oeil/Eudanla/IAC

we estimated adult survival rate without hunting to implement population models before investigating the impact of different hunting rates.

Stochastic population model using age-structured matrix

We modelled the fate of the flying-fox population with projections from a stochastic matrix model (female-based pre-breeding census) accounting for uncertainty in demographic parameters (Fig. 3; details in Appendix S5). This model did not incorporate density dependence in demographic rates. Overlooking this potential increase in survival and fecundity in response to hunting losses may overestimate the impact of hunting. However, long-lived species such as flying-foxes are expected to show little compensation for hunting mortality (Péron 2013). Moreover, this potential bias is compensated for, although to an unknown extent, by "crippling losses", i.e. animals wounded but not recovered by hunters and therefore not recorded in bags. Crippling losses may represent a significant proportion of hunting bags, particularly for pass-shooting at dusk (Clausen et al. 2017a).

We projected the size of the flying-fox population under varying hunting rates by simulating population trajectories and calculating the proportional change of the flying-fox population over 30 years. We explored values of the global hunting rate H_g, from which we derived age-specific hunting rates, between 0 and 10%. As juvenile survival (S_1) was unknown, we considered values ranging from 0.5 to 0.9. We further explored the relative merits of the alternative hunting regulations in improving population dynamics compared to the current situation with the median value of H_g. Age-specific hunting rates (H_1, H_2, H_{3+}) were kept constant across runs for each specific combination H_g *S_1, assuming that the number of flying-fox available influenced the number of hunters and the size of hunting bags (Peterson and Perez 2000). A stochastic population growth rate λ_s was calculated as the average across 30 years and across 5000 runs.

We further estimated the consequences of eight alternative hunting regulations as proposed to hunters in terms of hunting rate reduction (Appendix S6) and population

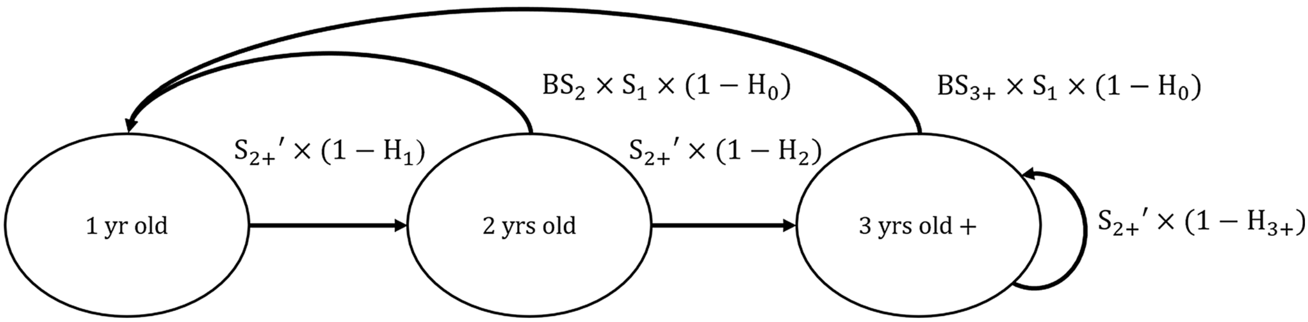

Fig. 3 Pre-breeding life cycle of flying-fox in New Caledonia. Population dynamics was modelled according to age-specific breeding success (*BS*), survival (*S*) and hunting rates (*H*). See Appendix S5 for details

trajectories over 30 years. We also tested for the combination of several regulations. It cannot be assumed, however, that new regulations will be strictly followed and responses to questionnaires indeed indicated that a proportion (though not estimable) of the bags was achieved illegally by exceeding the daily limit of kills and/or the hunting period. To account for the inherent uncertainty, we considered different ways in which hunters could respond to additional restrictions of their hunting. Specifically, we assumed that those hunting during a number of days below or above the legal limit would ignore new regulations in the same way. We estimated the expected reduction in total hunting bags for each regulation by considering that hunters with a number of hunting days within the limit would strictly follow new regulations, whereas hunters with a number of hunting days above the limits would either (1) not alter their (illegal) practices at all or (2) reduce it in proportion to the effort required. For the temporally recurrent ban and long-term moratorium, we assumed hunters would not increase their hunting effort when hunting is permitted. Regarding protected areas, we considered movements of individuals out of the protected area (Appendix S6).

All the analyses were performed on R 3.6.0 (R Core Team 2019).

RESULTS

Populations size, demographic rates, hunting bags and harvesting rates

We estimated the total population size for both *P. ornatus* and *P. tonganus* in New Caledonia, at 735 500 individuals before birth pulse (95% CI [421 000 – 1 060 500]). The proportion of females with a young averaged 0.79 ± 0.10 (mean weighted by sample size, $N = 311$). Age-at-death data revealed that hunting bags included 48% of young flying-foxes (< 1-year-old), 11% of age 1, 9% of age 2 and 32% of age 3+; Fig. 2). Regarding survival, the constant-risk model was best supported by the data and produced an average adult (from 1-year-old onwards, including hunting-related mortality) survival rate $S_{2+} = 0.78 \pm 0.10$ (Table 1).

Total number of hunters in the mainland of New Caledonia in 2019 was estimated at 10 291 [7897–12 685] of which 61.4% declared hunting flying-foxes (Appendix S4). Total hunting bags were estimated at 68 400 flying-foxes killed annually [53 800–83 200]. Therefore, the global hunting rate H_g imposed to flying-fox populations reached 7% [5.5 − 8.5]. Note that the current hunting regulation (5 flying-foxes per day per hunter over 8 days in April 2019) allowed theoretically for > 300 000 flying-foxes to be hunted annually.

Sensitivity of flying-foxes to hunting

We set the initial population size of flying-foxes at 368 000 females (i.e. the median population size). Adult survival rate (S_{2+}) obtained from age-at-death data was corrected for hunting mortality imposed to flying-foxes of age 1 and older to obtain hunting-free survival rates (for $H_g = 7.0\%$: $S_{2+\text{no\_hunt}} = 0.81$).

Using locally estimated breeding success and adult survival rate, the population model projected a growth rate $\lambda_i \approx 1$ for $S_1 > 0.64$ without hunting (Fig. 4). Further modelling results strongly suggests that the flying-fox population in New Caledonia is unlikely to survive the current level of hunting. Indeed, when considering S_{2+} impacted by the median H_g (7%), unrealistic values of S_1 are necessary to obtain $\lambda_s \approx 1$. Modelling based upon credible values of S_1 (< 0.8) indicated that the flying-fox population could sustain a global harvesting rate not larger than 2%, i.e. a quarter of that currently observed (Fig. 4).

Hunters' acceptance and demographic effectiveness of new hunting regulations

Due to the low resilience of flying-fox population to hunting (Fig. 4), none of the management alternatives per se allowed the population to display stable/increasing dynamics (Fig. 5a; Fig. S7). Considering a scenario with 'hunting as usual' (H_g = 7%), our model predicted a 79% decrease over 30 years. Substantial reductions (− 40%) of either the number of days where hunting is allowed or the maximal daily bag per hunter, provided only little improvement (reduction of 70–77% and 67–72%, respectively, according to the extent of illegal killing, see Methods), as did recurrent temporary hunting ban with frequency of one year out of three (66–69%) or four (68–71%). A recurrent temporary hunting ban with two years out of three appeared as the most successful strategy to slow the decline of the flying-fox population (44–55%). Concerning the establishment of protected areas, the protection of 10% of New Caledonia led to no improvement, whereas increasing the proportion to 25−40% yielded similar benefits to temporary hunting ban with frequencies of 1/3 and 2/3, respectively (Fig. 5a). Note that accounting for the specific response of hunters to new regulations according to their practices (legal vs. partially illegal) produces a substantial source of variation in the results. The level of illegal hunting may be large enough to entail a substantial population decline if maintained under a full hunting ban (Fig. 6). Considering the combination of several hunting regulations, the best option—including

Table 1 Summary of age-specific demographic rates, hunting bags and hunting rates of flying-foxes in New Caledonia

	Age 0	Age 1	Age 2	Age 3+
Breeding success	0	0	BS_{3+}− 0.60	0.79 ± 0.10
Survival rate	0.72	S_{2+} = 0.78 ± 0.10; S_{2+no_hunt} = 0.81		
Proportion in hunting bags	48%	11%	9%	32%
Hunting rate (for H_g = 7%)	35%	4%	5%	3%

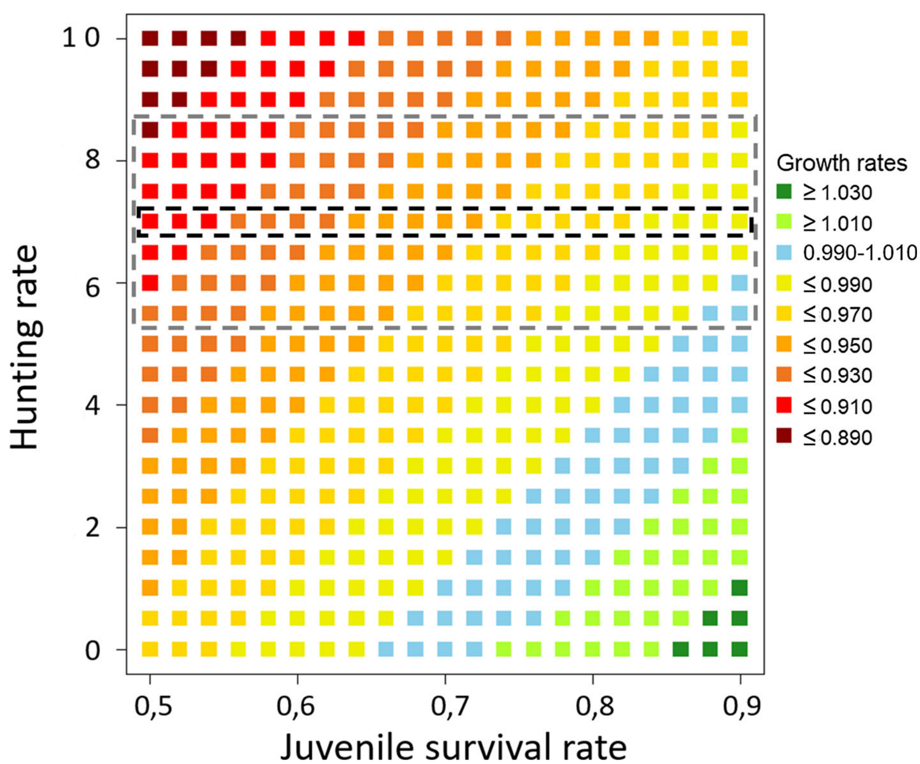

Fig. 4 Variation in stochastic population growth rates λ_s according to varying juvenile survival (S_1) and global harvesting rate (H_g) for flying-foxes in New Caledonia. Hunting bags derived from H_g were affected to the different age classes according to their relative sensitivity to hunting (see Methods). The other demographic rates were set at their average values with random noise (Table 1), as estimated using data collected in New Caledonia. The black and grey frames represent predictions corresponding to the median hunting rate (H_g = 7%) and lower/upper bounds of the 95% CI, respectively

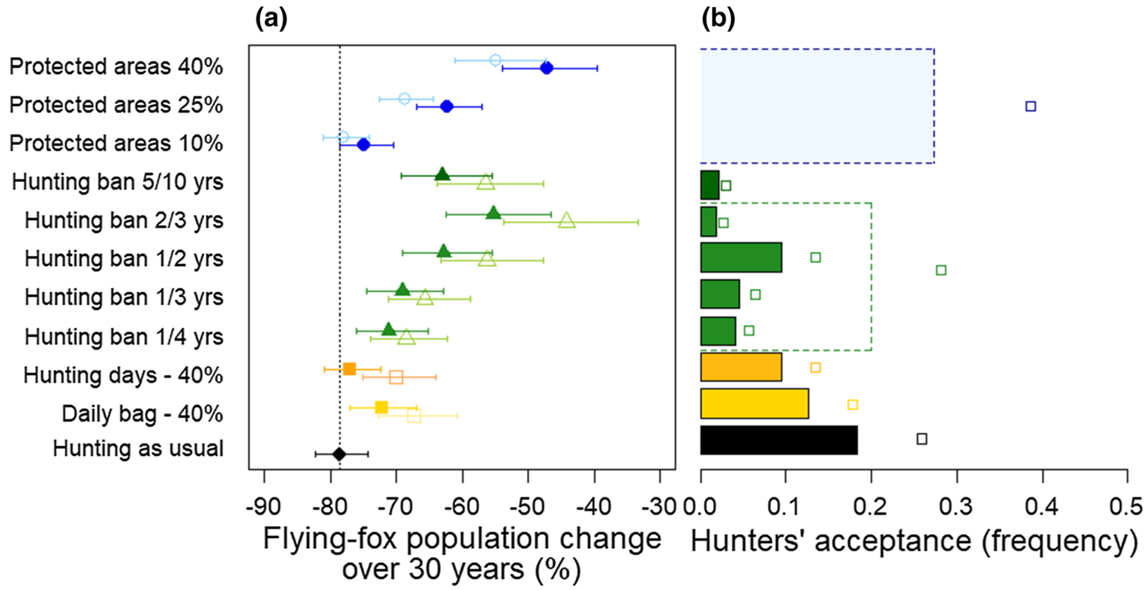

Fig. 5 **a** Predicted variation in flying-fox population size over 30 years in New Caledonia (median with 95% CI) according to current and proposed hunting regulations. Predictions were obtained from a stochastic model considering a median hunting rate H_g = 7% and juvenile and adult survival of 0.72 and 0.81, respectively. The extent of illegal hunting is accounted for by considering hunters who declared having exceeded the number of hunting days allowed would actually reduce their hunting activities in response to new regulations (dark colours) or not (light colours; see Methods). For protected areas, two hypotheses were tested with a report of the hunting bags outside protected areas (open circles) or not (filled circles). **b** Hunters' levels of acceptance for alternative hunting regulations calculated on 421 answers (bars) from 298 flying-fox hunters (squares). Note that hunters were not asked for the proportion of protected areas. The rectangle with green dotted lines indicates the cumulated answers for the short-term temporary hunting ban of any frequency. A remaining 14% of hunters (10% of votes) disagreed with all proposed regulations (not shown)

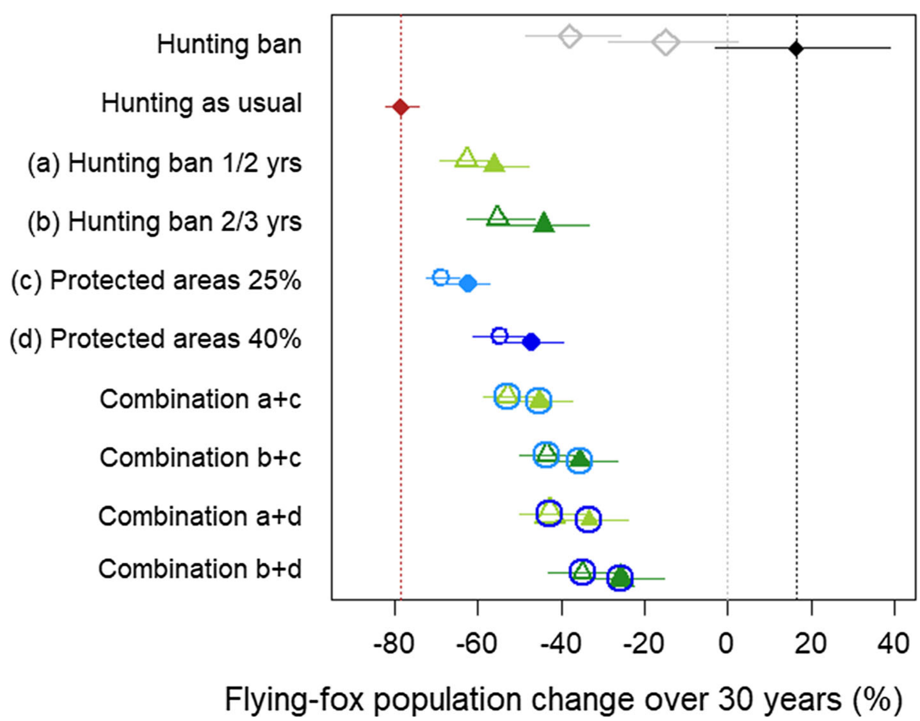

Fig. 6 Predicted variation in flying-fox population size over 30 years in New Caledonia (median with 95% CI) according to current and proposed hunting regulations in combination. Same specifications as for Fig. 5. The 'Hunting ban' option integrates the persistence of illegal hunting (grey symbols) or not (black symbol)

temporary ban of 2/3 years with 40% of protected areas—reduced the population decline over 30 years to 26–35%, i.e. still far from sustainability. Time series are shown in Appendix S7.

Among the 624 hunters who answered our questionnaire, 383 admitted hunting flying-foxes (61%). A total of 298 flying-fox hunters (i.e. 78%) provided usable answers regarding the onset of new regulations. A majority of them (60%) were ready to soften their practices and selected one (31%), two (20%) or three (9%) regulations (Fig. 5b). Twenty-six per cent answered that the current regulations were appropriate and the remaining 14% indicated that they agreed with none of the proposed new regulations. The preferred regulation was the implementation of protected areas, where flying-fox hunting would be banned, chosen by 39% of hunters and representing 27% of votes, followed by short-term temporary ban with 28% of hunters (20% of votes with 40 of 84 votes for the option 1/2 year). Long-term moratorium received the weakest support (3% of hunters, 2% of votes; Fig. 5b).

DISCUSSION

The issue of hunting sustainability in an era of a rapidly deteriorating environment is becoming more acute (Milner-Gulland and Bennett 2003; Weinbaum et al. 2013). Here we provide a first sustainability assessment of a hunting system involving bats (Berthinussen et al. 2020) and show that the hunting pressure currently imposed on flying-foxes in New Caledonia appears to be largely unsustainable. With a harvesting rate of 7%, and even accounting for the higher sensitivity to hunting of juveniles compared to adults, stochastic demographic projections indicate a severe decline of the population (− 79% over 30 years) and that the maximal sustainable hunting rate is probably < 2%. The majority of hunters, nevertheless, seem to be willing to soften their practices by accepting more restrictive regulations, such as the onset of protected areas or recurrent temporary hunting ban.

Does 'hunting as usual' remain sustainable in a rapidly changing world?

The current hunting rate applied to flying-foxes in New Caledonia was estimated to be four times higher than the population could sustain. Populations may respond to intense harvesting by altering life history traits, typically increasing reproduction in early age (Purvis 2001). We explored such a response by repeating the analysis presented in Fig. 4 with maximal reproductive rates from age 2 ($BS_2 = BS_{3+}$). Accounting for this, sustainable hunting rate increased from 2 to 4%, still far below the current level (Appendix S8). Results from model projections are in fact supported by empirical data indicating a loss of 33% of the numbers of roosts over the last 40 years (Oedin et al. 2019).

Bats are the only native land mammals of New Caledonia and flying-foxes were probably hunted by the first Melanesian people landing on the island 3200 years ago (Hand and Grant-Mackie 2012). Several changes have occurred recently that might explain why this long-standing hunting system is no longer sustainable. Flying-foxes still play a central role in the Kanak culture, being used as food for important ceremonies and sacred items, in addition to daily subsistence food. Flying-foxes are being less hunted for subsistence but remain a highly valued game animal and a key element of Kanak culture bas well as more recently settled communities. The recent addition of recreational hunting to the ancient but persistent traditional harvesting, mainly subsistence-related, has certainly been accompanied by a notable increase in hunting pressure. As an example, hunting of *P. vampyrus* doubled over a decade in Peninsular Malaysia (Epstein et al. 2009). Besides the replacement of traditional hunting tools by shotguns, the growing use of freezers has permitted storage and large-scale trade despite its prohibition. Meanwhile, the human population in New Caledonia has grown from 68 000 inhabitants in 1956 to 271 000 in 2019, a growth concerning all communities (Isee NC 2020). Concomitantly, humid forests, the main habitat used by flying-foxes, have shrunk by 72% contributing to the classification of New Caledonia as a Biodiversity Hotspot (Myers et al. 2000).

Invasive species, such as feral cats and yellow crazy ants (Palmas et al. 2017; Dorrestein et al. 2019; Oedin et al. 2021), and the expected increasing frequency of extreme climatic events with climate change (tropical storms, heat waves, bush fires; Welbergen et al. 2008; Westcott et al. 2018; Mo et al. 2020) may further affect bat population dynamics in tropical regions. Altogether, these multiple threats contribute to render hunting highly deleterious to flying-foxes (Vincenot et al. 2017; SPREP 2020). Most flying-foxes, however, are currently hunted or culled in the Indo-Pacific region (51 of the 59 *Pteropus*; IUCN 2020) and the issue of hunting sustainability is therefore critical for these species.

Vertebrate species with slow life history strategies, such as flying-foxes, are particularly vulnerable to additional anthropogenic mortality sources (Niel and Lebreton 2005; Péron 2013). Recent studies highlight the unsustainability of hunting concerning *P. rufus* and *Eidolon dupreanum* in Madagascar (Brook et al. 2019), *P. vampyrus* in Peninsular

Malaysia (Epstein et al. 2009), *P. tonganus* in Niue island, South Pacific (Brooke and Tschapka 2002) and *P. poliocephalus* in Australia (McIlwee and Martin 2002). On Guam, after centuries of coexistence with the indigenous Chamorro people, *P. tokudae*, endemic to the island, went extinct following the shift from subsistence to trade-based hunting promoted by Europeans (Wiles 1992). *P. mariannus* was nearly extirpated there for similar reasons (Monson et al. 2003). Overhunting has also contributed to the extinction of three of the four recently extinct *Pteropus* species and, with culling, remain a major threat for the extant species (IUCN 2020).

The socio-cultural context of New Caledonia renders a ban of flying-fox hunting, as it has been done in Samoa (Brooke 2001), unlikely and perhaps inefficient. Instead, we believe it might be wiser to build upon the high proportion of hunters willing to change their practices (60%) to implement sustainable management of bat hunting. A first step would consist in reaching an agreement on hunting regulations to obtain sustainable hunting bags. The sustainability of flying-fox hunting in New Caledonia would require a drastic reduction of annual hunting bags from 68 000 to 19 000 individuals to obtain a sustainable hunting rate ($< 2\%$). Our results indicate that only a combination of several regulations would sufficiently reduce hunting pressure to approach sustainability. From mixing results on modelled effectiveness and hunters' acceptance, it appears that the onset of protected areas together with a temporally recurrent hunting ban (1/2 year) could be a promising strategy. However, the effectiveness of protected areas depends on the proportion of the population under protection (Bowyer et al. 2019) and is hampered by the high mobility of flying-foxes (Welbergen et al. 2020) but also by the likely increased hunting pressure outside protected areas (Greenstreet et al. 2009). On the other hand, the extent of illegal practices a great deal of uncertainty about the effectiveness of the regulations and a strategy for increasing law enforcement is essential.

A key component of adaptive management is the collection of data to inform models and assess to what extent the objectives are fulfilled. The involvement of hunters is crucial for providing biological samples and data regarding their practices allowing one to monitor survival and hunting bags/rates in an efficient way. A successful strategy in the context of the Indo-Pacific region must further include customary regulations. Indeed, traditional management such as *Taboo* (prohibited access to bat roosts), seems to have been efficient in protecting flying-foxes by the past (Bräutigam and Elmqvist 1990). A hybrid management with an overlap between administrative and customary regulations might improve the acceptance of regulations and reduce the occurrence of illegal hunting (Aswani 2011; Rohe et al. 2017).

Combining demographic and sociological data into an adaptive management framework

Here we propose a framework integrating ecological, modelling and sociological data to reduce uncertainty around the implementation of new hunting regulations. In order to optimise the process of collecting hunting data, we designed an anonymous questionnaire aimed at estimating (1) individual hunting bags, (2) the level of compliance to current hunting regulations, and (3) the level of acceptance of alternative regulations (Watkins et al. 2018). Data collected on hunting bags obtained with this approach are possibly less accurate than those done with follow-up survey (Aubry and Guillemain 2019). Interestingly, hunting bags derived from the questionnaire were highly consistent with previous ones, based on a household consumption survey (Oedin et al. 2019). Furthermore, they provide data from which can be derived the level of non-compliance to hunting regulations, something out of reach with logbook data. The collection of such information was fully anonymous to maximise the recovery of honest answers. We collected answers from ca. 6% of the New Caledonian hunters within only four months. The confidence interval of global hunting rate [5.5−8.5%] estimated here fell in the lower range of the one estimated by Oedin et al. (2019; 5–14%), the latter considering the population size before the birth pulse, i.e. ignoring juveniles. We believe the comparison between expected demographic response of bats and hunters' acceptance of new regulations is a suitable method to improve hunting management issues as a decision support tool for managers. Gathering data on hunting practices is indeed crucial to optimise management by identifying both the most deleterious practices as well as new regulations that hunters are ready to accept.

CONCLUSIONS

Hunting appears as a major threat to flying-fox populations worldwide. Raising awareness about the ecological services provided by flying-foxes and their sensitivity to hunting is now critical to ensure their long-term conservation. Our work provides evidence for the low resilience of bat populations to hunting and offers an assessment of both the potential effectiveness of alternative hunting regulations and their level of acceptance by hunters. We believe such a multi-disciplinary approach, mixing ecological and social sciences, could be applied to other hunting systems, particularly in the Indo-Pacific region. In this region, growing human populations, and the associated shift from subsistence to recreational hunting, will increase pressure on natural resources, particularly on fragile island ecosystems. Adopting an adaptive management framework combining a detailed monitoring of hunted species and the involvement of all stakeholders, particularly hunters, for setting conservation objectives and management actions, could help to make hunting sustainable again.

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Author contribution MO, AM and FB designed the study. MO and FB coordinated data collection. MO and AM performed the modelling. MO, AM and FB wrote the manuscript and EV reviewed the final version.

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