Received: 14 July 2022 | Accepted: 30 January 2023

DOI: 10.1111/1365-2664.14376

Journal of Applied Ecology BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

Multiple co-occurring bioeconomic drivers of overexploitation can accelerate rare species extinction risk

Ryan J. Almeida[1] | **Juan A. Bonachela**[1,2] | **Julie L. Lockwood**[1,2]

[1]Graduate Program in Ecology & Evolution, Rutgers University, New Brunswick, New Jersey, USA

[2]Department of Ecology, Evolution, & Natural Resources, Rutgers University, New Brunswick, New Jersey, USA

Correspondence
Ryan J. Almeida
Email: rja149@sebs.rutgers.edu

Funding information
Rutgers School of Environmental & Biological Sciences; Rutgers Institute of Earth, Ocean, and Atmospheric Sciences

Handling Editor: Kulbhushansingh Suryawanshi

Abstract

1. The unsustainable harvest of species for the global wildlife trade is a major cause of vertebrate extinction. Through the anthropogenic Allee effect (AAE), overexploitation to extinction can occur when a species' rarity drives up its market price, enabling profitable harvest of all remaining individuals. Even in the absence of rarity value, however, the harvest of other species can subsidize the overexploitation of a rare species to the point of extinction, a phenomenon termed opportunistic exploitation. These two pathways to extinction have been considered independently, but many traded species experience them simultaneously.
2. In this study, we develop a simple model that incorporates these mechanisms simultaneously and demonstrate that including multiple harvest strategies with market-based feedbacks fundamentally alters rare species extinction risk and the rate at which overexploitation occurs. As a pertinent case study, we consider the harvest of ground pangolins *Smutsia temminckii*.
3. Our results show that pangolin extinction was generally associated with high rarity value, the use of multiple harvest strategies and the simultaneous harvest of a common species that has a fast life history. Pangolin population depletion and short-term extinction risk were greatest when harvesters used a combination of pursuit and opportunistic (i.e. multi-species) harvest strategies.
4. *Policy implications*. Our results suggest that feedbacks between multiple financial incentives to overharvest can exacerbate the risk of extinction of rare species. As a result, continuing to address AAE and opportunistic exploitation as separate extinction pathways may insufficiently capture extinction risk for many exploited species. Criteria for assessing extinction risk or harvest sustainability of exploited species should incorporate multiple drivers of harvest pressure, with an expanded focus on including species with high rarity value that are exploited in multi-species harvest regimes.

KEYWORDS
anthropogenic Allee effect, harvest model, opportunistic exploitation, overexploitation, pangolin, rarity value, Smutsia temminckii, wildlife trade

1 | INTRODUCTION

Wildlife trade threatens terrestrial vertebrate species with extinction, primarily via overexploitation (Maxwell et al., 2016). In the case of commercial trade, extinction risk often depends on whether harvest remains profitable as populations are depleted, since labour and opportunity costs associated with locating scarce prey impose financial burdens on harvesters preventing harvest to extinction (Branch et al., 2013; Chang & Drohan, 2018; Fa et al., 2002). When species have high enough market value, however, a plausible pathway to extinction via overexploitation is the anthropogenic Allee effect (AAE), which is a positive feedback loop whereby there is financial incentive to harvest a species as it becomes increasingly rare (i.e. rarity value; Courchamp et al., 2006). For an AAE to occur, a species must garner exorbitant selling prices when rare (Courchamp et al., 2006; Hall et al., 2008) since even moderately high rarity value can still result in a sustainable harvest (Holden & McDonald-Madden, 2017). This outcome suggests that for most species there is not sufficient financial payout for harvesters to justify investing resources into harvesting a population to extinction. However, rare species are seldom harvesters' exclusive target. Instead, flexibility and adaptability in species targeted can allow harvesters to ensure a steady source of income, often only including a rare species as opportunity arises (Branch et al., 2013; Clayton et al., 1997). Opportunistic exploitation can deplete populations at low abundances (Branch et al., 2013) providing another mechanism for exploitation to drive a species to extinction (Branch et al., 2013; Thurner et al., 2021). How feedbacks between the financial subsidy provided by opportunistic exploitation and rarity value impact rare species' extinction risk are unresolved. Here, we account for the ability of harvesters to employ both single-species and multi-species hunting strategies in a single model to assess whether multiple financial incentives to overharvest (i.e. both rarity value and opportunistic exploitation simultaneously) fundamentally alters the extinction risk of rare species compared to a single mechanism alone.

Harvest costs can increase with rarity because individuals that are scarce within a landscape require more effort, time or labour to catch (Grafton et al., 2007), or rare species may be put under law enforcement protection increasing costs to harvesters in avoiding enforcement efforts or paying fines (Milner-Gulland & Leader-Williams, 1992). The AAE helps explain how, if a rare species is valuable enough, financially motivated harvesters can swiftly deplete a population to extinction despite high harvest costs (Courchamp et al., 2006; Holden & McDonald-Madden, 2017; Siriwat et al., 2019). Species are only threatened with an AAE, however, when rarity value is high enough to offset rising harvest costs associated with increased rarity (Angulo et al., 2009; Courchamp et al., 2006; Holden & McDonald-Madden, 2017). In the absence of rarity value, profits from selling multiple common species can subsidize opportunistic harvest that would not be financially tenable when hunting only a single rare species. Because multi-species harvest is widespread, opportunistic harvest is likely the dominant threat to commercially exploited populations (Branch et al., 2013), as only the most valuable of species are profitable enough to be hunted alone.

When assessing the extinction risk of exploited species, these two mechanisms (the AAE and opportunistic exploitation) have typically been considered as separate pathways to extinction. However, for species at risk of an AAE, it is likely inevitable that high rarity value will incentivize hunters to opportunistically poach. Hunter behaviour can be fluid, and hunters use multiple strategies, gears and techniques to increase their probability of capturing a specific species or increase the range of species they target in pursuit of higher profits (Branch et al., 2013; Dobson et al., 2019). Additionally, species that are relatively easy to capture may be exploited by both single-species and multi-species hunters at the same time. Opportunistic exploitation may cause hunters to deplete populations of species that exhibit modest rarity value but would have been too expensive to harvest below the anthropogenic Allee threshold using only a single-species approach (Courchamp et al., 2006; Holden & McDonald-Madden, 2017). This feedback could widen the range of species at risk of an AAE, as opportunistic exploitation would increase the number of species that can be profitably hunted at low abundances. Alternatively, sudden increases in market value could incentivize opportunistic poaching of species that otherwise might not typically be worth a hunters' effort, thus triggering an additional source of harvest pressure that can accelerate the effects of AAE. This feedback suggests that, while AAE and opportunistic exploitation theory may sufficiently explain extinction risk on the margins, for some species extinction risk can depend on feedbacks between these two mechanisms.

We explore this middle ground between the AAE and opportunistic exploitation by integrating these two mechanisms of extinction into a single simple model of exploitation. Importantly, because multi-species harvest is pervasive (Branch et al., 2013; Thurner et al., 2021) and international consumer demand for high value wildlife continues to grow ('t Sas-Rolfes et al., 2019), the dynamics captured by this model could apply to many species with rarity value that are hunted alongside other species and/or hunted using multiple techniques. As a demonstrative case study, we parameterize our model to the harvest of ground pangolins *Smutsia temminckii* and explore the influence of harvester strategy and bioeconomic feedbacks on its extinction risk. Pangolins (order: Pholidota) are among the most heavily exploited animals on the planet and sold within legal and illegal markets (Heinrich et al., 2016; Ingram et al., 2018). Due to lack of breeding programmes, pangolin trade is fuelled entirely by wild-sourced animals (Challender et al., 2019; Hua et al., 2015), and international trafficking of the declining wild populations to meet consumer demand has driven up selling prices in the past 20 years. Additionally, because most populations exist at low densities and pangolins are typically nocturnal and shy (Heinrich et al., 2016), flexibility in harvest strategy is essential to successful hunting (e.g. Aisher, 2016; D'Cruze et al., 2018; Ingram et al., 2018), with shotgun pursuit, hand harvest and trapping/snaring being the most popular techniques used to hunt pangolins (Ingram et al., 2018).

2 | MATERIALS AND METHODS

2.1 | General harvest model

We adapt a framework used by Holden and McDonald-Madden (2017) to describe human harvest effort/pressure, E, on a focal species population of size N_1, and a common species population of size N_2. In our version of the model, a population of harvesters can engage in a mix of two harvest strategies: pursuit harvest and opportunistic harvest (Figure 1). Pursuit harvest means that only the focal species is being harvested, and thus harvester effort and costs are tied only to the dynamics of that single species. By contrast, opportunistic harvest means that the focal species is not the harvester's only target; rather, the harvester exploits both the common and focal species, and only harvests the focal species if encountered; but continues to do so as it becomes increasingly rare. We assume that opportunistic harvest leads to roughly a constant income gained from harvesting and selling the common species over time, with some variation from year to year (see *Incorporating variability*).

Our model linking the dynamics of the focal species to the total effort a harvester devotes to both pursuit and opportunistic harvest follows the equations:

$$\frac{dN_1(t)}{dt} = r_1N_1\left(1 - \frac{N_1}{K_1}\right) - sq_1N_1E - (1-s)\gamma N_1E, \tag{1}$$

$$\frac{dN_2(t)}{dt} = r_2N_2\left(1 - \frac{N_2}{K_2}\right) - (1-s)q_2N_2E, \tag{2}$$

$$\frac{dE(t)}{dt} = \alpha\left[s\left(P\left(N_1\right)q_1N_1E - cE\right) + (1-s)\left(P\left(N_1\right)\gamma N_1E + p_0q_2N_2E - c_0E\right)\right]. \tag{3}$$

The first term in Equation (1) represents population growth for the focal species at a maximum rate r_1, with limitations imposed by a carrying capacity K_1; the second and third terms represent pursuit and opportunistic harvest, respectively, with s being the proportion of effort dedicated to pursuit harvest in a year (and, thus, a fraction $1–s$ to opportunistic harvest). It is important to note that s simply represents the average proportion of effort the population of hunters placed exclusively on the focal species over a certain time period, and therefore some variation is possible at the level of individual hunters year after year (see section *Incorporating variability* below). Similarly, the first term in Equation (2) represents population growth for the common species, with a maximum growth rate of r_2 and a carrying capacity of K_2, and the second term represents targeted harvest for the common species (which may lead to opportunistic hunting of the focal species).

Equation (3) represents changes in total population effort over time, where the first term represents the net income (i.e. gross income minus costs) obtained from pursuit harvest, and the second term represents the net income obtained from the combination of income from the focal species, income from the common species and costs of opportunistic harvest. $P(N_1)$ is the price function for the focal species, which here depends on the population size (see below). The sale of the common species, on the other hand, provides the harvester with an additional income, p_0. It is important to note that, while the assumption of a constant income source ignores potential price-abundance dynamics associated with hunting the common species, it allows easy exploration of how opportunistic harvest

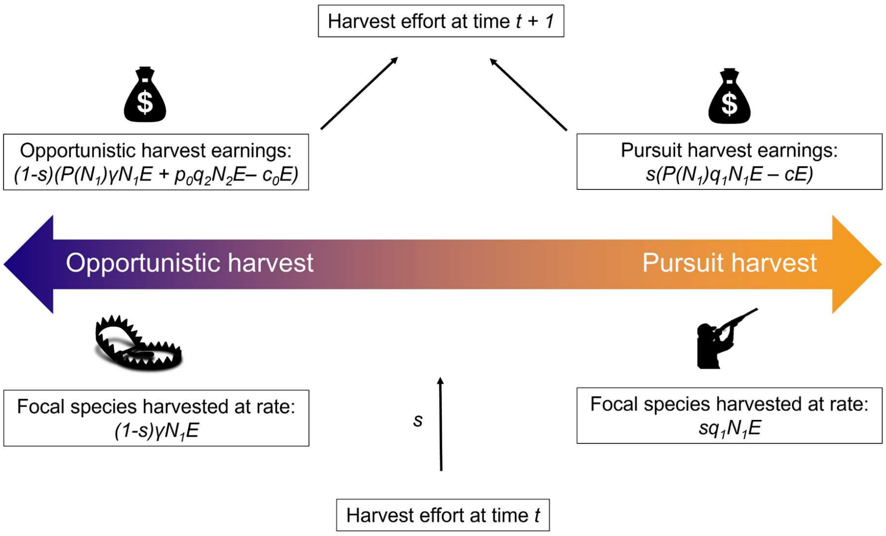

FIGURE 1 Conceptual framework describing the contributions of harvest strategy to harvest effort. In our model, harvest strategy s determines the partition of total effort between pursuit harvest (occurring at a proportion of total effort s) and opportunistic harvest (occurring at a proportion of total effort $1–s$). The net income earned from harvesting and selling species using these two strategies is pooled and used to fund the harvesters' next harvest expedition. When $s = 0$, the harvester engages in opportunistic harvest, whereas when $s = 1$ the harvester engages only in pursuit harvest. We symbolize pursuit harvest with gun hunting and opportunistic harvest with trapping as these are two common techniques used to harvest pangolins (see Section 2.4).

can directly subsidize overexploitation, as described by theory (Branch et al., 2013). The effect of market information on harvester effort is encoded using a constant conversion factor α, where higher values indicate that total harvest effort is more sensitive to changes in market dynamics. We assume that pursuit harvest leads to greater yield of the focal species than opportunistic harvest ($q_1 > \gamma$), but the cost per unit effort is also higher ($c > c_0$) (Branch et al., 2013). See Table S1 for parameter values and units.

2.2 | Incorporating an AAE

When market price is insensitive to rarity, $P(N_1) = p$, that is, there is no AAE. We incorporate the AAE into our framework by assuming a price–abundance relationship (Holden & McDonald-Madden, 2017):

$$P(N_1) = a + \frac{b}{N_1^{\,z} + 1}, \tag{4}$$

where a represents the minimum price paid per individual of the focal species, $b+a$ is the price of individuals of the focal species at a quasi-extinction threshold ($P(N_1 = N_e)$) and higher values of z increase the sensitivity of market price to changes in the focal species' abundance. Harvest regimes with both high z (e.g. $z > 1$) and b indicate a strong AAE (Holden & McDonald-Madden, 2017).

This price–abundance relationship makes calculating generalized expressions for the equilibria of the model more complicated. Although analytical solutions can be determined for select values of z (e.g. Holden & McDonald-Madden, 2017), for our pangolin harvest example (which includes stochasticity as explained next) we analysed our model numerically using a customized forward Euler integration scheme in R (R Core Team, 2022).

2.3 | Incorporating variability

While several of our parameters are assumed to be constant over time, it is reasonable to expect variation in certain parameter values at short time-scales. For example, we assume the partitioning of harvest effort among the two harvest strategies (s) to be constant over time but, in reality, there is likely variation in harvesters' strategy choices within and throughout the years (Dobson et al., 2019). Likewise, we assume a constant stream of income from harvesting a common species (p_0) over the course of the dynamics but, within any given year, this alternative source of income can vary with several socioeconomic and ecological factors (e.g. local market volatility, competition from other hunters). In our study, we incorporated modest stochasticity in these two key components of opportunistic harvest to capture this variation. To do so, we randomly drew parameter values at each timestep from a normal distribution whose mean is the parameter value presented in Table S1 (see next section).

An additional source of stochasticity is environmental variability, which can cause a rare species' population dynamics to differ considerably from baseline equilibrium predictions (e.g. Melbourne & Hastings, 2008). In the case of ground pangolins, numerous population-level threats including habitat loss, electrocution via electric fences and gin traps that may cause population sizes to fluctuate outside of harvest and natural population dynamics (Pietersen et al., 2014a). Here, we captured the influence of non-harvest threats and environmental variability generally by incorporating a simple additive noise term to both the focal and common species' population sizes,

$$gN\,\sigma(t), \tag{5}$$

where g is a constant and σ is a random number that follows the standard normal distribution.

2.4 | Ground pangolin parameter estimates

We parameterized our model to the poaching of the South African ground pangolin *Smutsia temminckii* population to demonstrate how opportunistic harvest and the AAE can influence the dynamics of an exploited species in tandem. We used recent estimates of ground pangolin population size and demography derived from field research in South Africa (Pietersen et al., 2014a, 2014b, 2016, 2020; Table S1). We paired these data with market and socioeconomic surveys of pangolin harvest (Boakye et al., 2016; D'Cruze et al., 2018; Ingram et al., 2018, 2019; Table S1). For parameters where pangolin-specific data are lacking, we derived estimates from previous models and socioeconomic harvest studies that focus on similar taxa, regions and markets (e.g. Damania et al., 2005; Holden & McDonald-Madden, 2017; Rogan et al., 2018; Rowcliffe et al., 2003; Table S1).

Similarly, while detailed life-history and harvest data exist for many species, little is known about the biology and harvest dynamics of the vast majority of species threatened with overexploitation in the wildlife trade (Fukushima et al., 2020; Scheffers et al., 2019; 't Sas-Rolfes et al., 2019). Additionally, while opportunistic harvest is often framed as a 'two-species' system, harvesters in this system often hunt several common species at once (Martins & Shackleton, 2019; Rogan et al., 2018), and can switch between focal species, making identifying a single common species that subsidizes opportunistic ground pangolin harvest a challenge. As a result, we elected to use generalized vertebrate life-history parameters (e.g. Pearson et al., 2014; Rowcliffe et al., 2003) to explore the dynamics of the common species (Table S1). We parameterized our model using two life-history categories (e.g. Rowcliffe et al., 2003): a slow-reproducing species with slow growth rate, and a fast-reproducing species with rapid population growth rate. While it is unclear exactly which species are subsidizing ground pangolin harvest in reality, slow life-history species could represent large ungulates such as African buffalo or blue wildebeest, a common target of bushmeat hunters, while fast life-history species could include prolific species that are commonly sold in markets, such as duikers (e.g. Hayward, 2009;

Martins & Shackleton, 2019). We analysed our model numerically for both pangolin and common species harvest dynamics, focusing our analyses primarily around the dynamics of the pangolin population, since it is the species of conservation concern.

For two parameters associated with rarity value, selling price at extinction (*b*) and the price-abundance scaling factor (*z*), virtually no data are available, as little is known about the realized relationship between selling price and abundance for most commercially harvested species (Holden & McDonald-Madden, 2017). When *z* and *b* are relatively large values (e.g. $z > 1$), price is highly sensitive to changes in abundance, and species are likely to be harvested to extinction as described by AAE theory (Courchamp et al., 2006; Holden & McDonald-Madden, 2017). While the selling price of pangolin scales and meat is rising (Challender et al., 2015), assessing the sensitivity of the price–abundance relationship for pangolin species is a challenge due to the lack of reliable abundance estimates across time (Heinrich et al., 2016). Thus, we explored both low sensitivity (i.e. low rarity value) and high sensitivity (i.e. high rarity value) price–abundance scenarios.

2.5 | Equilibrium analysis

We simulated ground pangolin population size and harvest effort for a range of *s* values between solely opportunistic ($s = 0$) and solely pursuit ($s = 1$) harvest strategies. The solely opportunistic harvest ($s = 0$) scenario represents opportunistic exploitation as described by Branch et al. (2013) and Thurner et al. (2021), while the solely pursuit harvest scenario ($s = 1$) corresponds to classical AAE theory (Courchamp et al., 2006). Intermediate values of *s* represent harvest scenarios where both opportunistic and pursuit harvest are used. For each of these harvest scenarios, we simulated pangolin harvest dynamics that co-occurs with harvest of either a slow life-history common species or a fast life-history common species, until the system reached stationarity under three price conditions: constant price (i.e. Equation (4) with $z = 0$, $b = 0$), low rarity value (i.e. Equation (4) with $z = 0.5$, $b = 3.8 \times 10^4$) and high rarity value (i.e. Equation (4) with $z = 1.5$, $b = 9.2 \times 10^8$). Under a constant price scenario, pangolin selling price does not vary with abundance (i.e. no rarity value, $P(N) = a$, Courchamp et al., 2006). Alternatively, under low and high rarity value scenarios, ground pangolin selling price rises as the population is depleted, presenting the possibility of an AAE (Equation (3); Figure S1). For this and all subsequent analyses, we run $n_{sim} = 1000$ simulations, assume a quasi-extinction threshold $Ne = 10$, and no stochasticity. For scenarios that led to extinction, we calculated an average time to extinction by averaging number of years it took the pangolin population to cross our quasi-extinction threshold (i.e. $N(t) < N_e$) across all simulations.

2.6 | Pangolin short-term extinction risk

For each *s* value, we calculated a probability of extinction (p_e) for ground pangolins, defined as the proportion of simulations ($n_{sim} = 1000$) in which the population crosses our quasi-extinction threshold, N_e. We repeated these calculations for the two common species life-history types, and for each of the three price–abundance scenarios. We also measure population depletion by calculating the proportion of the starting population size remaining at the end of each simulation, with values of 1 indicating $N_1(t) \geq N_1(t = 0)$, and values less than 1 indicating $N_1(t) \leq N_1(t = 0)$. We allow the simulations to run for 50 years and allow a modest amount of stochasticity in harvest strategy (i.e. *s* is a random Gaussian number with mean *s* and variance 0.15). Exploring short-term dynamics (as opposed to only equilibrium states) is important from a conservation perspective, as identifying which harvest strategies and other drivers of overexploitation accelerate rates of population depletion can inform the prioritization of conservation efforts and policy. We chose a 50-year time window to capture a snapshot of short-term dynamics; while 50 years of harvest is an arbitrary benchmark, restricting our analyses to a much shorter time-scale (e.g. 25 years) may fail to capture any extinctions that may occur. Alternatively, increasing this time-scale will capture more extinctions, but would be less illustrative in showing which strategies pose the most immediate extinction risk.

2.7 | Model sensitivity

Because there is a considerable amount of uncertainty in published data on pangolin biological and harvest parameters, we also explored how short-term extinction risk varies across a large range of values for our parameters. For each parameter, we took the low rarity value scenario and slow life-history common species scenario parameter values (Table S1) used in our short-term extinction risk analysis and multiply them by factors ranging from 0.001 to 1000 according to a logarithmic scale (e.g. 0.001, 0.01, 0.1) to obtain a new parameter value. For each of these new parameter values, we then determined p_e after 50 years of simulations across a range of different *s* values while keeping all other parameters constant as listed in Table S1. In all sensitivity simulations, we also assumed $g = 0.05$, and stochasticity in both p_0 and *s* (see above). The complete results of our sensitivity analysis are shown in Appendix S6 of the Supporting Information (Figure S7).

3 | RESULTS

3.1 | Equilibrium analysis

When harvester used only a single harvest strategy (i.e. $s = 0$, pure opportunistic harvest, or $s = 1$, pure pursuit harvest), stationary states were largely dependent on the life-history type of the common species and the strategy used. Pure opportunistic harvest led to sustainable harvest of both the pangolin and the common species when the common species exhibited a slow life-history type, regardless of rarity value (Figure S3). When the common species was a fast life-history type, pure opportunistic harvest led to extinction of both species regardless of rarity value (Figure S4). Alternatively, when harvesters used pure pursuit harvest, pangolin harvest was sustainable when pangolins had a constant selling price or exhibited low rarity value, while high rarity value was unprofitable for harvesters (Figures S3 and S4). In all cases, pure pursuit harvest allowed the common species to reach carrying capacity, since only the pangolin was being harvested.

When harvesters engaged in both opportunistic and pursuit harvest (i.e. values of s between 0 and 1), stationary states varied depending on the extent to which each strategy was used and the life-history type of the common species (Figure 2). With a constant price (i.e. no AAE), pangolin were driven extinct when the common species exhibited a fast life history regardless of the harvest strategy, except for pure pangolin pursuit harvest (i.e. $s = 1$, no harvest of common species). When price was held constant and the common species had a slow life-history type, pangolin populations persisted, with strategies incorporating both pursuit and opportunistic harvest leading to the lowest pangolin population sizes (Figure 2). When incorporating a modest price–abundance relationship (i.e. low rarity value), equilibrium pangolin population sizes were generally lower than the constant price scenario. Otherwise, the qualitative pattern of dynamics with respect to harvest strategy and common species life-history remained consistent between no rarity value and modest rarity value. When selling price was highly sensitive to abundance (i.e. high rarity value), however, pangolin extinction was far more common. When harvesters hunted pangolins and a slow life-history common species, pangolins were driven extinct for a range of s-values incorporating both opportunistic and pursuit harvest ($0.22 \le s \le 0.97$). For pure or nearly pure pursuit harvest ($s \ge 0.98$), however, pangolin harvest was not profitable (i.e. harvest effort was driven to zero), and pangolins persisted at carrying capacity. When the common species exhibited a fast life history, pangolins were driven extinct for all values of s; except for pure pursuit harvest ($s = 1$), which was unprofitable for harvesters (Figure 2). Stationary

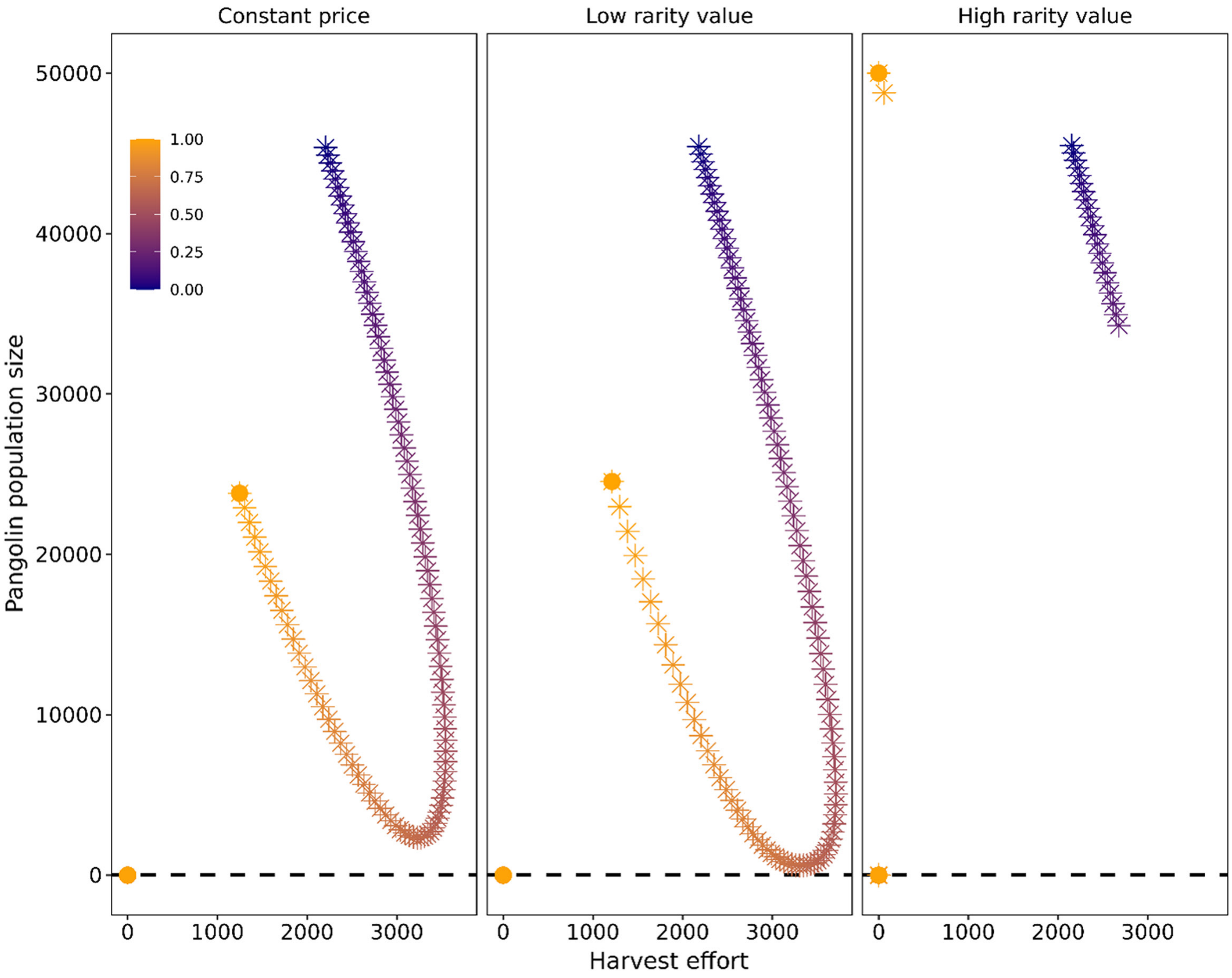

FIGURE 2 Influence of harvest strategy on equilibrium values of pangolin population size (N) and harvest effort (E). We simulated pangolin harvest dynamics for a range of harvest strategies (s-values, colour scale) under three market conditions (constant price, low rarity value and high rarity value) with two co-harvested common species having one of two life-history types: slow (stars) and fast (points). Here we allowed the simulations to reach stationarity and assumed no stochasticity. Dashed line at $N = 10$ indicates quasi-extinction threshold (N_e).

states for the common species exhibited qualitatively similar patterns to the pangolin population with respect to bioeconomic scenario (Figure S5).

3.2 | Short-term extinction risk

Analysis of short-term pangolin extinction probabilities (50 years) revealed differing effects of harvest strategy, price variability and common species life-history type on extinction risk. When harvesters exploited both pangolins and a fast life-history common species, pangolins were not driven extinct. When the common species exhibited a slow life history, however, extinction risk was dependent on harvest strategy and price variability (Figure 3). When price was held constant, the pangolin population was not driven extinct in the short term, but population depletion occurred for increasing effort devoted to pursuit harvest, s. The most severe depletion occurred when harvesters engaged in a combination of opportunistic and pursuit harvest (Figure 3, 'Constant price'; $s = 0.68$; mean population reduction = 94.18%). This pattern remained when pangolins exhibited low rarity value, with the most severe population depletion occurring at $s = 0.70$ (Figure 3, 'Low rarity value'; mean population reduction = 99.40%). When pangolins exhibited high rarity value, extinction occurred for intermediate s values (Figure 3, 'High rarity value'; $0.09 \leq s \leq 0.82$), with extinction risk being highest when harvesters engaged in a relatively similar amount of pursuit and opportunistic harvest ($P_e = 1$ for $0.35 \leq s \leq 0.62$). Extinction occurred in an average of 39.15 years, and harvest strategies that led to the highest extinction risk corresponded with the fastest extinction times (mean time to extinction = 34.93 years for $0.35 \leq s \leq 0.62$).

4 | DISCUSSION

Previous attempts to model overexploitation to extinction have treated the AAE and opportunistic harvest as independent mechanisms, reducing harvester behaviour to a single aspect (Damania et al., 2005; Holden & McDonald-Madden, 2017; Rowcliffe et al., 2003). However, this assumption is likely too narrow given that many species are exploited in multi-species harvest systems (Bi et al., 2017; Chang & Drohan, 2018). Focusing on the harvest and sale of ground pangolins as a case study, we show that, when considered in tandem, AAE and opportunistic harvest lead to increased and accelerated extinction risk compared to either mechanism alone. When selling prices remained constant or varied modestly with pangolin population size, opportunistically harvesting pangolins alongside a fast life-history common species enabled harvesters to exploit pangolins to extinction over long time-scales, supporting prior research (Branch et al., 2013; Thurner et al., 2021). Conversely, pure pursuit harvest or opportunistic harvest alongside slow life-history common species did not lead to pangolin extinction. When pangolin selling price was highly sensitive to abundance (i.e. AAE conditions), pure opportunistic harvest or strategies incorporating both opportunistic and pursuit harvest led to pangolin extinction over long time scales. Critically, combining opportunistic and pursuit harvest drove pangolins extinct over relatively short time scales

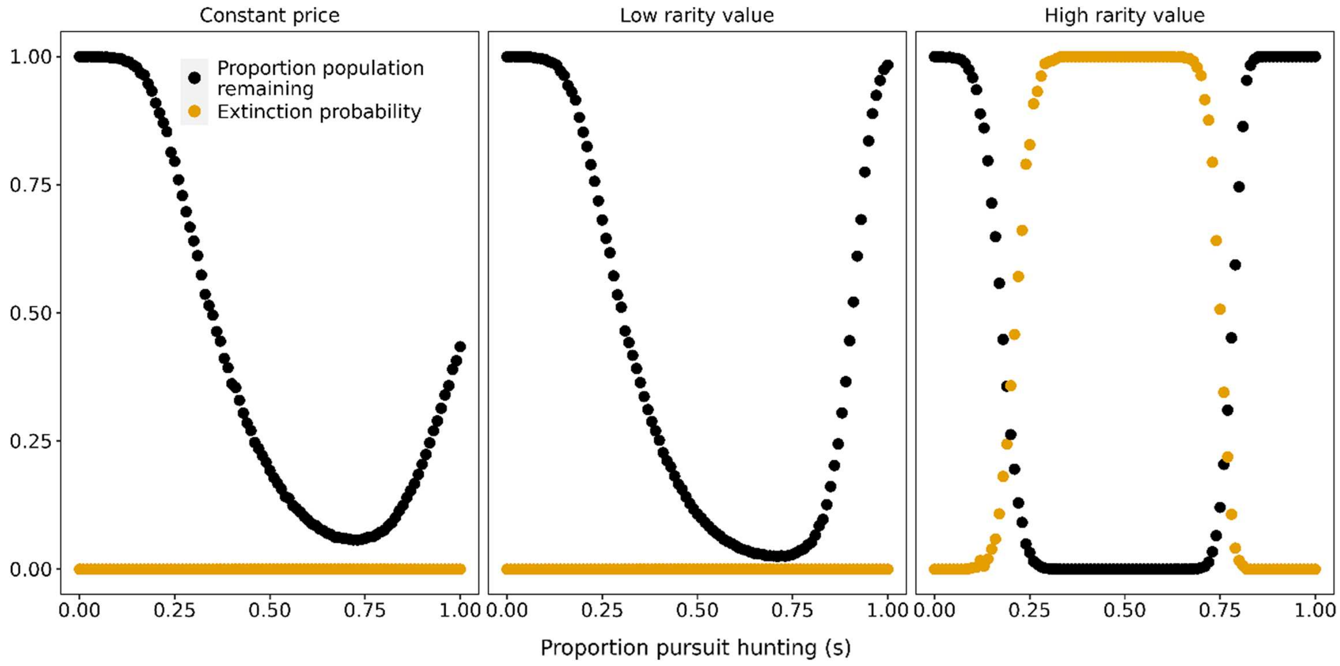

FIGURE 3 Impact of harvest strategy on short-term extinction risk with slow life-history common species co-exploitation. We simulated extinction probability (yellow) and average proportion of initial population size remaining (black) for a ground pangolin population after 50 years of simulated harvest. Extinction probability is the proportion of simulations ($n = 1000$) that end in extinction after 50 years of simulated harvest under constant and variable price scenarios. Complete list of parameter values is listed in Table S1.

when rarity value was high. Furthermore, strategies relying on relatively equal amounts of pursuit and opportunistic harvest posed the highest short-term extinction risk to pangolins, and drove pangolins extinct at the shortest time-scales. Our results suggest that assessing rare species extinction risk according to either the AAE or opportunistic exploitation alone can underestimate the rate and severity of decline caused by harvest.

Numerical analysis of our model demonstrated that pangolin extinction risk was primarily associated with high rarity value and the use of multiple harvest strategies. In the absence of rarity value, opportunistic harvest could still lead to pangolin extinction if harvesters obtained sufficient subsidy from harvesting common species. Even in the case where a species exhibits rarity value, the question of how populations reach a sufficiently low population size to trigger the Allee effect. In the absence of a non-harvest related driver of population decline, Holden and McDonald-Madden (2017) suggest that a sufficient minimum selling price can enable harvesters to deplete a population below the AAE threshold. We build on this finding by demonstrating that when this minimum selling price is low, profits from hunting other species can provide an alternative financial subsidy that allows harvesters to drive an abundant population below the AAE threshold. These results add to a growing body of evidence that opportunistic exploitation is a viable threat to harvested species, supporting both bioeconomic theory (Branch et al., 2013) and previous modelling studies incorporating opportunistic exploitation (Thurner et al., 2021). Moreover, our model follows previous approaches in portraying opportunistic harvest as a 'two-species system', where the harvest of a single common species subsidizes the opportunistic harvest of a rare species. In reality, however, harvesters can hunt and sell substantially more than two species (Chang & Drohan, 2018; Damania et al., 2005; Rowcliffe et al., 2003). While we addressed this uncertainty by exploring dynamics where the common species followed one of two life-history types, our model structure is most well suited to situations where harvest dynamics are known to be closely tied to two species, such as the opportunistic snaring of babirusa during wild pig hunts in Sulawesi (Clayton et al., 1997). We suggest that elaborations of models of opportunistic harvest should explore how the dynamics of several common species impact the exploitation of a rare species.

By employing both opportunistic and pursuit harvest strategies, harvesters in our model were able to sustain higher levels of harvest effort (i.e. higher profits) than either strategy alone could support. This increased harvest effort increased the magnitude and the rate of overexploitation, highlighting the potential for interactions between multiple bioeconomic drivers of extinction risk. In our model, we chose to exogenously define a (fixed) average proportion of time/effort that harvesters devoted to one versus the other harvest strategy, *s*, which represents an annual average of the hunter's strategy, with allowing some within-year variation. This assumption may be most appropriate to conservation policy scenario planning (Peterson et al., 2003) when considering large populations of hunters, or if the motivation for hunters to use one or the other strategy is unknown. However, in reality, financially motivated hunters are far more likely to alternate between harvest strategies until settling on a strategy that optimizes their hunting profits depending on market conditions and the species being hunted (i.e. variable *s*, with changes being motivated by the optimization of effort and profits). Future studies are needed to understand how financially motivated, forward-looking hunters alter harvest strategy in response to market and ecological feedbacks (Dobson et al., 2019). In biodiverse regions where many species are sold for profit, protecting an imperilled species from overexploitation could require regulating the harvest of co-occurring species (Branch et al., 2013). However, the efficacy of such regulations remains unresolved, and likely depends heavily on the behavioural responses of hunters to new regulation and subsequent downstream effects on the hunters' payout for harvest.

To our knowledge, ours is the first attempt to use harvest models to assess the sustainability of the international pangolin trade. This gap is likely due to the paucity of published data on pangolin population dynamics and trade, especially among the four African species. For example, opportunistic harvest catchability is challenging to assess in situ, as illicit poaching behaviour is often clandestine (Barber-Meyer, 2010), harvest yields depend heavily on the harvest technique used (Dobson et al., 2019), and capture success likely varies with the behaviours and perceptions of individual hunters (Thurner et al., 2021). However, our model is relatively robust to changes in opportunistic harvest catchability, with pangolins' short-term extinction risk only modestly changing following a 100× increase in this catchability parameter. As a result, only a rough approximation of opportunistic harvest catchability may suffice to assess pangolin harvest dynamics. Comparatively, our model was more sensitive (although still relatively robust) to the parameterization of market traits such as the selling price of pangolins and other species. These findings underlay the importance of conducting market surveys to track selling prices of harvested species (e.g. Boakye et al., 2016; Challender et al., 2015; Nijman et al., 2016). Data from these local studies should be collated to develop accurate price estimates (e.g. Ingram et al., 2018) when using models to inform management and specific policy recommendations.

We chose pangolin harvest for our analysis because they are highly exploited, potentially at risk of an AAE (Aisher, 2016; Challender et al., 2015), and hunted using several different harvest strategies (D'Cruze et al., 2018; Ingram et al., 2018; Pietersen et al., 2014a). It is likely that there are many exploited species sharing these characteristics, and as a result our findings may be generalizable to species that share a consumer base (e.g. ivory, tiger parts), display rarity value, co-occur with other highly exploited species (e.g. in biodiverse regions) and/or have slow life-history characteristics (e.g. elephants, rhinoceroses). We recognize that exploitation alone does not a priori drive species to extinction, and, when managed within a robust evidence-based governance structure, can provide positive incentives for conservation and contribute to recovery of imperilled populations (Challender et al., 2021; Hutton & Leader-Williams, 2003). However, our results show that whether commercial harvest leads to extinction depends on a suite of factors, including the degree of flexibility in strategy choice exhibited by the harvester, species-specific rarity–price relationships, and the profit gained from the capture and sale of co-occurring species.

AUTHOR CONTRIBUTIONS

Ryan J. Almeida and Julie L. Lockwood conceived the ideas. Ryan J. Almeida and Juan A. Bonachela designed and conducted the analyses. Ryan J. Almeida led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

ACKNOWLEDGEMENTS

Ryan J. Almeida was supported by the Rutgers School of Environmental & Biological Sciences and the Rutgers Institute of Earth, Ocean, and Atmospheric Sciences during this work. We would like to thank P. McElwee, P. Morin and anonymous reviewers for their helpful comments on the manuscript.

CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

Data and code associated with this study available from the Dryad Digital Repository https://doi.org/10.5061/dryad.0p2ngf25b (Almeida et al., 2023).

ORCID

Ryan J. Almeida https://orcid.org/0000-0003-3400-0052
Juan A. Bonachela https://orcid.org/0000-0002-3316-8120
Julie L. Lockwood https://orcid.org/0000-0003-0177-449X

REFERENCES

Aisher, A. (2016). Scarcity, alterity and value: Decline of the pangolin, the World's Most trafficked mammal. *Conservation and Society*, *14*(4), 317. https://doi.org/10.4103/0972-4923.197610

Almeida, R. J., Bonachela, J. A., & Lockwood, J. L. (2023). Data from: Multiple co-occurring bioeconomic drivers of overexploitation can accelerate rare species extinction risk. *Dryad Digital Repository*. https://doi.org/10.5061/dryad.0p2ngf25b

Angulo, E., Deves, A.-L., Saint Jalmes, M., & Courchamp, F. (2009). Fatal attraction: Rare species in the spotlight. *Proceedings of the Royal Society B: Biological Sciences*, *276*(1660), 1331–1337. https://doi.org/10.1098/rspb.2008.1475

Barber-Meyer, S. M. (2010). Dealing with the clandestine nature of wildlife-trade market surveys. *Conservation Biology*, *24*(4), 918–923. https://doi.org/10.1111/j.1523-1739.2010.01500.x

Bi, S. G., Koné, I., Béné, J. C. K., Bitty, E. A., Yao, K. A., Kouassi, B. A., & Gaubert, P. (2017). Bushmeat hunting around a remnant coastal rainforest in Côte D'ivoire. *Oryx*, *51*(3), 418–427. https://doi.org/10.1017/S0030605315001453

Boakye, M. K., Kotzé, A., Dalton, D. L., & Jansen, R. (2016). Unravelling the pangolin bushmeat commodity chain and the extent of trade in Ghana. *Human Ecology*, *44*(2), 257–264. https://doi.org/10.1007/s10745-016-9813-1

Branch, T. A., Lobo, A. S., & Purcell, S. W. (2013). Opportunistic exploitation: An overlooked pathway to extinction. *Trends in Ecology & Evolution*, *28*(7), 409–413. https://doi.org/10.1016/j.tree.2013.03.003

Challender, D. W. S., Brockington, D., Hinsley, A., Hoffmann, M., Kolby, J., Masse, F., Natsuch, D., Oldfield, T., Outhwaite, W., 't Sas-Rolfes, M., & Milner-Gulland, E. J. (2021). Mischaracterising wildlife trade and its impacts may mislead policy processes. *Conservation Letters*, *15*(1), e12832. https://ora.ox.ac.uk/objects/uuid:2609a2c5-59e1-4f02-a8e1-4b8682864317

Challender, D. W. S., Harrop, S. R., & MacMillan, D. C. (2015). Understanding markets to conserve trade-threatened species in CITES. *Biological Conservation*, *187*, 249–259. https://doi.org/10.1016/j.biocon.2015.04.015

Challender, D. W. S., Sas-Rolfes, M., Ades, G. W. J., Chin, J. S. C., Ching-Min Sun, N., Chong, J. I., Connelly, E., Hywood, L., Luz, S., Mohapatra, R. K., de Ornellas, P., Parker, K., Pietersen, D. W., Roberton, S. I., Semiadi, G., Shaw, D., Shepherd, C. R., Thomson, P., Wang, Y., … Nash, H. C. (2019). Evaluating the feasibility of pangolin farming and its potential conservation impact. *Global Ecology and Conservation*, *20*, e00714. https://doi.org/10.1016/j.gecco.2019.e00714

Chang, C. H., & Drohan, S. E. (2018). Should I shoot or should I go? Simple rules for prey selection in multi-species hunting systems. *Ecological Applications*, *28*(8), 1940–1947. https://doi.org/10.1002/eap.1796

Clayton, L., Keeling, M., & Milner-Gulland, E. J. (1997). Bringing home the bacon: A spatial model of wild pig hunting in Sulawesi, Indonesia. *Ecological Applications*, *7*(2), 642–652. https://doi.org/10.1890/1051-0761(1997)007[0642:BHTBAS]2.0.CO;2

Courchamp, F., Angulo, E., Rivalan, P., Hall, R. J., Signoret, L., Bull, L., & Meinard, Y. (2006). Rarity value and species extinction: The anthropogenic Allee effect. *PLoS Biology*, *4*(12), e415. https://doi.org/10.1371/journal.pbio.0040415

Damania, R., Milner-Gulland, E. J., & Crookes, D. J. (2005). A bioeconomic analysis of bushmeat hunting. *Proceedings of the Royal Society B: Biological Sciences*, *272*(1560), 259–266. https://doi.org/10.1098/rspb.2004.2945

D'Cruze, N., Singh, B., Mookerjee, A., Harrington, L. A., & Macdonald, D. W. (2018). A socio-economic survey of pangolin hunting in Assam, Northeast India. *Nature Conservation*, *30*. https://ora.ox.ac.uk/objects/uuid:19aa64a2-85dd-479 e-9362-eb874372d435, 83–105.

Dobson, A. D. M., Milner-Gulland, E. J., Ingram, D. J., & Keane, A. (2019). A framework for assessing impacts of wild meat hunting practices in the tropics. *Human Ecology*, *47*(3), 449–464. https://doi.org/10.1007/s10745-019-0075-6

Fa, J. E., Peres, C. A., & Meeuwig, J. (2002). Bushmeat exploitation in tropical forests: An intercontinental comparison. *Conservation Biology*, *16*(1), 232–237. https://doi.org/10.1046/j.1523-1739.2002.00275.x

Fukushima, C. S., Mammola, S., & Cardoso, P. (2020). Global wildlife trade permeates the tree of life. *Biological Conservation*, *247*, 108503. https://doi.org/10.1016/j.biocon.2020.108503

Grafton, R. Q., Kompas, T., & Hilborn, R. W. (2007). Economics of overexploitation revisited. *Science*, *318*(5856), 1601. https://doi.org/10.1126/science.1146017

Hall, R. J., Milner-Gulland, E. J., & Courchamp, F. (2008). Endangering the endangered: The effects of perceived rarity on species exploitation. *Conservation Letters*, *1*(2), 75–81. https://doi.org/10.1111/j.1755-263X.2008.00013.x

Hayward, M. W. (2009). Bushmeat hunting in Dwesa and Cwebe nature reserves, eastern cape, South Africa: Research article. *South African Journal of Wildlife Research - 24-Month Delayed Open Access*, *39*(1), 70–84. https://doi.org/10.10520/EJC117305

Heinrich, S., Wittmann, T. A., Prowse, T. A. A., Ross, J. V., Delean, S., Shepherd, C. R., & Cassey, P. (2016). Where did all the pangolins go? International CITES trade in pangolin species. *Global Ecology and Conservation*, *8*, 241–253. https://doi.org/10.1016/j.gecco.2016.09.007

Holden, M. H., & McDonald-Madden, E. (2017). High prices for rare species can drive large populations extinct: The anthropogenic Allee effect revisited. *Journal of Theoretical Biology*, *429*, 170–180. https://doi.org/10.1016/j.jtbi.2017.06.019

Hua, L., Gong, S., Wang, F., Li, W., Ge, Y., Li, X., & Hou, F. (2015). Captive breeding of pangolins: Current status, problems and future prospects. *Zookeys*, *507*, 99–114. https://doi.org/10.3897/zookeys.507.6970

Hutton, J. M., & Leader-Williams, N. (2003). Sustainable use and incentive-driven conservation: Realigning human and conservation interests. *Oryx*, *37*(2), 215–226. https://doi.org/10.1017/S0030605303000395

Ingram, D. J., Coad, L., Abernethy, K. A., Maisels, F., Stokes, E. J., Bobo, K. S., Breuer, T., Gandiwa, E., Ghiurghi, A., Greengrass, E., Holmern, T., Kamgaing, T. O. W., Obiang, A.-M. N., Poulsen, J. R., Schleicher, J., Nielsen, M. R., Solly, H., Vath, C. L., Waltert, M., … Scharlemann, J. P. W. (2018). Assessing Africa-wide pangolin exploitation by scaling local data. *Conservation Letters*, *11*(2), e12389. https://doi.org/10.1111/conl.12389

Ingram, D. J., Cronin, D. T., Challender, D. W. S., Venditti, D. M., & Gonder, M. K. (2019). Characterising trafficking and trade of pangolins in the Gulf of Guinea. *Global Ecology and Conservation*, *17*, e00576. https://doi.org/10.1016/j.gecco.2019.e00576

Martins, V., & Shackleton, C. M. (2019). Bushmeat use is widespread but under-researched in rural communities of South Africa. *Global Ecology and Conservation*, *17*, e00583. https://doi.org/10.1016/j.gecco.2019.e00583

Maxwell, S. L., Fuller, R. A., Brooks, T. M., & Watson, J. E. M. (2016). Biodiversity: The ravages of guns, nets and bulldozers. *Nature News*, *536*(7615), 143–145. https://doi.org/10.1038/536143a

Melbourne, B. A., & Hastings, A. (2008). Extinction risk depends strongly on factors contributing to stochasticity. *Nature*, *454*(7200), Article 7200. https://doi.org/10.1038/nature06922

Milner-Gulland, E. J., & Leader-Williams, N. (1992). A model of incentives for the illegal exploitation of black rhinos and elephants: Poaching pays in Luangwa Valley, Zambia. *Journal of Applied Ecology*, *29*(2), 388–401. JSTOR. https://doi.org/10.2307/2404508

Nijman, V., Zhang, M. X., & Shepherd, C. R. (2016). Pangolin trade in the Mong La wildlife market and the role of Myanmar in the smuggling of pangolins into China. *Global Ecology and Conservation*, *5*, 118–126. https://doi.org/10.1016/j.gecco.2015.12.003

Pearson, R. G., Stanton, J. C., Shoemaker, K. T., Aiello-Lammens, M. E., Ersts, P. J., Horning, N., Fordham, D. A., Raxworthy, C. J., Ryu, H. Y., McNees, J., & Akçakaya, H. R. (2014). Life history and spatial traits predict extinction risk due to climate change. *Nature Climate Change*, *4*(3), 217–221. https://doi.org/10.1038/nclimate2113

Peterson, G. D., Cumming, G. S., & Carpenter, S. R. (2003). Scenario planning: A tool for conservation in an uncertain world. *Conservation Biology*, *17*(2), 358–366. https://doi.org/10.1046/j.1523-1739.2003.01491.x

Pietersen, D. W., Jansen, R., Swart, J., Panaino, W., Kotze, A., Rankin, P., & Nebe, B. (2020). Chapter 11—Temminck's pangolin Smutsia temminckii (Smuts, 1832). In D. W. S. Challender, H. C. Nash, & C. Waterman (Eds.), *Pangolins* (pp. 175–193). Academic Press. https://doi.org/10.1016/B978-0-12-815507-3.00011-3

Pietersen, D. W., McKechnie, A. E., & Jansen, R. (2014a). A review of the anthropogenic threats faced by Temminck's ground pangolin, Smutsia temminckii, in southern Africa. *South African Journal of Wildlife Research*, *44*(2), 167–178. https://doi.org/10.3957/056.044.0209

Pietersen, D. W., McKechnie, A. E., & Jansen, R. (2014b). Home range, habitat selection and activity patterns of an arid-zone population of Temminck's ground pangolins, Smutsia temminckii. *African Zoology*, *49*(2), 265–276. https://doi.org/10.1080/15627020.2014.11407642

Pietersen, D. W., Symes, C. T., Woodborne, S., McKechnie, A. E., & Jansen, R. (2016). Diet and prey selectivity of the specialist myrmecophage, Temminck's ground pangolin. *Journal of Zoology*, *298*(3), 198–208. https://doi.org/10.1111/jzo.12302

R Core Team. (2022). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.R-project.org/

Rogan, M. S., Miller, J. R. B., Lindsey, P. A., & McNutt, J. W. (2018). Socioeconomic drivers of illegal bushmeat hunting in a southern African savanna. *Biological Conservation*, *226*, 24–31. https://doi.org/10.1016/j.biocon.2018.07.019

Rowcliffe, J. M., Cowlishaw, G., & Long, J. (2003). A model of human hunting impacts in multi-prey communities. *Journal of Applied Ecology*, *40*(5), 872–889. https://doi.org/10.1046/j.1365-2664.2003.00841.x

Scheffers, B. R., Oliveira, B. F., Lamb, I., & Edwards, D. P. (2019). Global wildlife trade across the tree of life. *Science*, *366*(6461), 71–76. https://doi.org/10.1126/science.aav5327

Siriwat, P., Nekaris, K. A. I., & Nijman, V. (2019). The role of the anthropogenic Allee effect in the exotic pet trade on Facebook in Thailand. *Journal for Nature Conservation*, *51*, 125726. https://doi.org/10.1016/j.jnc.2019.125726

't Sas-Rolfes, M., Challender, D. W. S., Hinsley, A., Veríssimo, D., & Milner-Gulland, E. J. (2019). Illegal wildlife trade: Scale, processes, and governance. *Annual Review of Environment and Resources*, *44*(1), 201–228. https://doi.org/10.1146/annurev-environ-101718-033253

Thurner, S. D., Converse, S. J., & Branch, T. A. (2021). Modeling opportunistic exploitation: Increased extinction risk when targeting more than one species. *Ecological Modelling*, *454*, 109611. https://doi.org/10.1016/j.ecolmodel.2021.109611

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: **Almeida, R. J., Bonachela, J. A., & Lockwood, J. L. (2023). Multiple co-occurring bioeconomic drivers of overexploitation can accelerate rare species extinction risk.** *Journal of Applied Ecology*, *00*, 1–10. https://doi.org/10.1111/1365-2664.14376