

Stressor equivalents: A framework to prevent perverse outcomes in data-poor systems

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ABSTRACT

Environmental systems suffer from multiple interacting stressors. Each stressor can act on
different parts of the system and at different time scales. This hampers measuring and predicting
the stressors' impacts on ecosystems. We propose a conceptual method that integrates available data
with physical constraints over relevant time scales to predict management outcomes in data-scarce

51 systems affected by multiple stressors. We first predict the combined stressor levels that threaten a
52 management target and then define *stressor equivalents* to convert between. These “ball-park”
53 estimates of critical stressor levels help to identify how the threat posed by interacting stressors
54 responds to its management. Our approach assists managers in the decision-making process
55 regarding when to manage a system and how to monitor. We illustrate our concept with a case
56 study of an invaded island ecosystem, yet our approach is useful for other data-poor environmental
57 systems that suffer from multiple cumulative stressors.

58 INTRODUCTION

59 Environmental stressors occur across a range of spatial and temporal scales (Brook et al. 2008;
60 Brown et al. 2013). Stressors commonly interact in three different ways; additively, antagonistically
61 or synergistically (Côté et al. 2016). Additive stressors have a cumulative effect, which is the sum
62 of the individual effects. Coral reefs, for example, are threatened by the interaction of ocean
63 acidification, poor water quality, over-fishing, thermal stress and severe weather events (De’ath
64 et al. 2012). In antagonistic systems, the presence of one stressor mitigates the negative effect
65 of another stressor. For example, the olfactory senses of sharks are negatively affected by ocean
66 acidification. However, when sharks are negatively affected through ocean warming, additional
67 ocean acidification mitigates these impacts (Pistevos et al. 2017). Synergistic stressors benefit from
68 the presence of other stressors, resulting in worse effects on the system than the simple addition of
69 both stressors (Crain et al. 2008; Klein et al. 2010). Corals, for example, can become hyper-sensitive
70 to warming when they are already stressed by poor water quality (Carilli et al. 2009).

71 Knowing the consequences of management prior to any action is useful for choosing the best
72 conservation intervention (Dietze et al. 2018). Unfortunately, we often lack information about the
73 environmental systems. Learning about a system requires time and resources for monitoring and
74 experiments, which may be unavailable when urgent action is required (Stem et al. 2005). To
75 tackle pressing issues in complex systems with multiple interacting stressors and data scarcity, we
76 developed a conceptual methodology that simplifies a complex system to its core components and
77 investigates how multiple stressors acting over different timescales affect a management target. Our

approach uses "stressor equivalents" to integrate multiple stressors and assesses critical stressor levels that would jeopardize the positive effect of a management action. Thereby we change the question from, "What will happen to the system after a particular management intervention?", to the more specific, "What conditions are likely to have negative consequences for the management target?". To overcome the lack of system specific data, we combine estimates from other systems with physical constraints and information about the timescales over which stressors act. This limits the number of possible predictions to a realistic range and yields "ball-park" estimates for critical stressors.

While the above issues occur in any complex system, we focus on a case study of an invaded ecosystem. Invasive species are among the five key drivers of ecosystem change (IPBES 2019) and represent one of the largest challenges to global biosphere integrity (Steffen et al. 2015). Therefore, management of invasive species has become a priority for many government and non-government conservation initiatives (e.g., feral cats in Australia (Department of the Environment, Australia 2015) or predator-free New Zealand 2050 (Department of Conservation, New Zealand 2017)). While this well-intended investment aims at conserving threatened species, studies have demonstrated potential for unintended consequences when managing only one of several invasive species (Rayner et al. 2007; Bergstrom et al. 2009; Ritchie & Johnson 2009; Caut et al. 2009; Courchamp et al. 2011; Wittmer et al. 2013; Prior et al. 2018). For example, eradicating feral cats from Little Barrier Island in New Zealand led to a habitat-specific increase in rat predation on seabirds (Rayner et al. 2007). In a different case, previously unobserved predation by rats on sooty terns (*Sterna fuscata*) became apparent after the management of cats (Hughes et al. 2019). Predictive models like the one we present here can help to evaluate the conditions that could lead to unintended consequences from predator control, and can help design informed monitoring programs.

On Christmas Island multiple invasive species, including feral cats (*Felis catus*) and black rats (*Rattus rattus*), prey on a number of native species (Beeton et al. 2010). Due to the high risk posed by these invaders, a cat control program commenced on the island in 2010 with plans for a rat

eradication program to follow (Algar & Hamilton 2014). Since cats also eat rats, the two stressors may interact antagonistically. Controlling cats could therefore have perverse consequences for native species, if it leads to a mesopredator release of rats (Beeton et al. 2010; Han 2016; Baker et al. 2018). We simplify the Christmas Island system to its core stressors (i.e., cats and rats) and focus on one threatened species (i.e., red-tailed tropicbirds, *Phaethon rubricauda*, Fig. 1). For this three-species system, we investigate the conditions under which the cat control would lead to negative consequences for the bird population. Life history and other relevant knowledge of the three interacting species were obtained from Christmas Island (where possible) or other locations that harbour these species (Table S1). We further use physical limitations, such as energetic requirements and energy content of the species, to develop a mechanistic and life stage-structured model to predict changes in the bird population, depending on the number of predators in the system. This life-history model captures important timescales of cat and rat predation and bird breeding biology to assess the critical predation threat to the bird population. Our model identifies the critical size of predator populations (alone and combined), an equivalence between the two stressors, and important model parameters for designing a monitoring program. While invasive species provide a globally important example, our conceptual methodology applies to any environmental system affected by multiple interacting stressors such as species populations affected by habitat fragmentation, harvesting and climate warming (Mora et al. 2007).

METHODS

To demonstrate our conceptual methodology for integrating multiple stressors on a target system, we chose an invasive species case study from Christmas Island, Australia. Our aim was to identify the conditions under which eradicating one invasive species was likely to be ineffective or counterproductive in protecting a target native species. Christmas Island is a 135km² Australian territory in the Indian Ocean. Feral cats (*Felis catus*) and invasive black rats (*Rattus rattus*) arrived within the last 100 years and have since integrated themselves into the island's food web, which includes numerous other invasive species. Like cats, rats predate on native species such as the red-tailed tropicbird (*Phaethon rubricauda*), but they also serve as a food source for cats and native

birds of prey. Eradicating cats may allow rats to reproduce without limitation by cats leading to a mesopredator release of rats (Soule et al. 1988). On other island, changes in rat populations or behaviour have caused negative outcomes for native species after controlling cats (e.g., (Rayner et al. 2007; Hughes et al. 2019)).

Red-tailed tropicbirds are medium-sized seabirds occurring on islands and coastal regions of the tropics of the Indian and Pacific Oceans. While red-tailed tropicbirds spend most of their lives at sea, they nest on the ground, where they are vulnerable to terrestrial predation, by predators including cats and rats. After reaching reproductive maturity around three years of age, each breeding pair typically produces one egg per season until the end of their lifespan around 13–16 years (Schreiber & Schreiber 1993). The Australian population of red-tailed tropicbirds is classified as near threatened. Its largest population occurs on Christmas Island and has been declining over the past 20 years, likely due to predation by invasive species (Ishii 2006). On Christmas Island, limited resources (i.e., personnel, funding etc.) and high environmental complexity (e.g., dense rain forest vegetation, sharp cliffs) pose major constraints on estimating the population sizes of red-tailed tropicbirds, cats and rats. Managers may therefore not detect a decline in the population of the target species until it is too late.

The model

To assess the predation pressure of feral cats and rats on the population of red-tailed tropicbirds, we develop a mechanistic model for the bird population that accounts for births, natural mortality and predation by cats and rats. The model considers the predation rate by cats and rats at different stages of the seabird's life cycle: while rats consume eggs and hatchlings (juvenile birds in nest), cats kill hatchlings and adult birds. We assume the daily predation from cats and rats to be constant throughout the bird's relatively short breeding period on the island. We assessed the fate of the tropicbird population with a measure of reproductive success, η , that accounts for both short-term changes in adult bird population due to direct cat predation in the breeding season, and longer-term impacts of egg and hatchling predation (see Eq. 1). After the juveniles fledge, all birds leave the island and spend their time offshore to forage until they return to breed. Birds return to the island

for the first time after reaching reproductive maturity (Fleet 1974).

The purpose of our model is three-fold: first, to define the combined levels of cat and rat populations which seriously threatens the bird species (critical stressor level). Second, to identify the number of rats which put the same amount of pressure on the bird population as a single cat ("cat equivalent"). Lastly, to identify the number of rats that would alone threaten the persistence of the bird population. Thus, even if managers do not have accurate assessment of the population size of target species, our model illustrates both quantitatively and qualitatively what predator numbers will threaten the red-tailed tropicbird population.

A key challenge is finding a suitable persistence indicator for the target species because the two predator species impact different life stages, and there is not enough information to parameterize a full life-cycle model. We resolve this issue by quantifying the reproductive success, η of red-tailed tropicbirds (Eq. 1) as the ratio of juvenile birds hatched in the current breeding season who survive to reproductive maturity three years later ($N_{J,3}$), compared to the decrease in adult bird population over the first breeding season, i.e., the difference between the adult population at the start ($N_{A,0}$) and end ($N_{A,1}$) of the breeding season:

$$\eta = \frac{N_{J,3}}{N_{A,0} - N_{A,1}}. \quad (1)$$

If η is below one, then the mortality rate (due to natural mortality and predation) is larger than the reproduction and hence the population of red-tailed tropicbirds is declining over time. Above one the population is increasing.

We calculated the change in adult population over the first breeding season, $N_{A,0} - N_{A,1}$ based on the adult bird population at the start of the breeding season $N_{A,0}$, annual natural adult mortality μ_A , the size of the cat populations N_{Cats} , the duration of the breeding season T_B , during which time the birds were exposed to predation, and the number of adult birds consumed per cat per day $p_{A,C}$ as:

$$N_{A,0} - N_{A,1} = N_{A,0} \mu_A + N_{Cats} p_{A,C} T_B. \quad (2)$$

The number of juveniles hatching in year one $N_{A,1}$, who survive to reproduce after year three $N_{J,3}$, depends on the initial population of breeding birds $N_{A,0}$, the number of eggs laid per adult bird β , the egg viability (proportion of eggs that hatch) ν , the number of eggs eaten per rat per day $p_{E,R}$, the number of hatchlings (juvenile birds after hatching and before leaving the nest) eaten per cat and rat per day $p_{H,C}$ and $p_{H,R}$, respectively, the egg incubation time T_I and the duration that hatchlings spend in the nest T_H , where $T_B = T_I + T_H$:

$$N_{J,3} = \nu (\beta N_{A,0} - N_{Rats} p_{E,R} T_I)(1 - \mu_H) - N_{Cats} p_{H,C} T_H - N_{Rats} p_{H,R} T_H(1 - \mu_J)^{T_{mat}}. \quad (3)$$

Equation 3 arises from a mass balance of the juvenile population until they become reproductively mature $N_{J,3}$, adjusted for the initial hatchling mortality $(1 - \mu_H)$, and fledgling mortality (juveniles after leaving the nest and before becoming reproductively mature) $(1 - \mu_J)^{T_{mat}}$. Here, μ_J describes the annual juvenile mortality and T_{Mat} refers to the time that fledglings spend off the island until they become reproductively mature. We used published estimates for the parameters in Eqs. 2 and 3 from Christmas Island where possible, and otherwise with literature information from other systems and energetic limitations on metabolic rates.

Little data exist on the current population sizes of predators or prey on Christmas Island. Since a full dynamic model could not be reliably parameterized, initialized or verified, we developed a simpler model based on three key principles. Instead of predicting all possible outcomes, the purpose of our model is to identify the conditions which threaten the population of red-tailed tropicbirds. Therefore, we devised a model that can pool the stressors into a single predation indicator, here *cat-equivalents*. Further, our model uses the simplest possible assumptions on thermodynamic constraints (i.e., metabolic demands and body mass) and species-specific information from Christmas Island and other locations (i.e., prey preferences, birds biology). We examined the literature for comparable systems and specified parameters as the physical limitations with an energy system approach (see below). Please refer to Table 1 for an overview of model parameters, their units, values and sources.

We defined reasonable limits to all parameters based on either data from CI or other systems. Where no information was available we allowed a variation of $\pm 20\%$ around the mean estimate of each parameter value (Tab. 1). We distinguish three classes of parameters: parameters that relate to reproduction and mortality, parameters that relate to predation, and energetic parameters.

These parameters can capture seasonal and environmental changes, e.g. varying climate or resource availability. We calculated the predation rates (Eqs. 5-7) of cats and rats on the different life stages of red-tailed tropicbirds. These equations provide the number of prey individuals consumed per day by an individual predator (prey / day*predator) using estimates from other systems (Tab. 1). Throughout the equations we used letters to refer to cats (C), rats (R), adult birds (A), hatchlings (H), and eggs (E). The equations are based on the energetic demand of predators $MetDemand_C$, $MetDemand_R$; the energy contents of prey items $Energy_E$, $Energy_H$, $Energy_A$; the masses of the species $Mass_C$, $Mass_R$, $Mass_E$, $Mass_H$ and $Mass_A$; and finally the daily proportion of each predator's diet that is adult bird, hatchling or egg, $PreyPref_{A,C}$, $PreyPref_{H,C}$, $PreyPref_{H,R}$, $PreyPref_{E,R}$. The energetic demand of a predator is based on its mass (see Tab. 1). This approach minimizes the number of system parameters to a relatively small set of parameters, which are observable by managers.

$$p_{A,C} = \frac{MetDemand_C[\frac{kJ}{cat*day}] \times PreyPref_{A,C}}{Mass_A[\frac{g}{bird}] \times Energy_A[\frac{kJ}{g}]} \quad (4)$$

$$p_{J,C} = \frac{MetDemand_C[\frac{kJ}{cat*day}] \times PreyPref_{J,C}}{Mass_J[\frac{g}{bird}] \times Energy_J[\frac{kJ}{g}]} \quad (5)$$

$$p_{J,R} = \frac{MetDemand_R[\frac{kJ}{rat*day}] \times PreyPref_{J,R}}{Mass_J[\frac{g}{bird}] \times Energy_J[\frac{kJ}{g}]} \quad (6)$$

$$p_{E,R} = \frac{MetDemand_R[\frac{kJ}{rat*day}] \times PreyPref_{E,R}}{Mass_E[\frac{g}{egg}] \times Energy_E[\frac{kJ}{g}]} \quad (7)$$

Stressor phase space

The model outlined above does not seek to predict the impact of the cat population on the rat population; rather, we define a *stressor phase space* based on predator population sizes for which the bird population increases, declines or remains stable. The cat and rat populations in Eqs. 2 and 3 are therefore constant. To disentangle the cumulative effects of the two stressors (i.e., cats and rats) on the persistence of the red-tailed tropicbird population, we solve Eqs. 2 and 3 for the reproductive success required for a stable population ($\eta=1$). This resulted in two measures; the number of rats, which would put the bird population at risk in absence of any cats (*CriticalRats*, Eqn. 8) and the number of rats that correspond to the same effect on the reproductive success as one cat (*CatEquivalents*, Eqn. 9).

$$\text{CriticalRats} = \frac{N_{A,0} \nu \beta(1 - \mu_J) - \eta N_{A,0} \mu_A (1 - \mu_J)^{-T_{Mat}}}{p_{J,R} T_H + \nu(1 - \mu_H) p_{E,R} T_I}; \quad (8)$$

$$\text{CatEquivalents} = \frac{p_{J,C} T_H + p_{A,C} \eta T_B (1 - \mu_J)^{-T_{Mat}}}{p_{J,R} T_H + \nu(1 - \mu_H) p_{E,R} T_I}. \quad (9)$$

These equations are subject to the following constraints:

- The number of adults at the end of the breeding season is non-negative;
- The number of eggs that were laid during the current breeding season and that survive the incubation period is non-negative;
- The number of juveniles that were born in the current breeding season and that survive as hatchlings is non-negative.

Parameter uncertainty and sensitivity of cat equivalents

Many of the specific estimates for the parameter values were not available for the study site. To account for parameter uncertainty, we either used reported ranges or assumed 20% around the reported mean estimate of the parameter value. We then approximated the uncertainty with the Monte Carlo simulation (Xiao et al. 2017) and used the probability distributions of the outputs

to construct uncertainty bounds for the model predictions. We assumed that the probability distributions of all literature estimates of the model parameters were independent of each other. Thereby, we identified the 95% and 68% credible intervals for stable reproductive rate in the stressor phase space (Fig. 1, main document, border line between blue and red shades) and the uncertainty distributions of cat equivalents and critical rat numbers (Fig. 5). We therefore define reasonable limits to all parameter estimates based on literature estimates from other systems, and physiological constraints based on energy requirements (Table S1). Where the literature only delivers mean estimates, we allow 20% variation around the estimate (see Supplementary Methods). We propagated this uncertainty through to the model outputs with the Monte Carlo method (after (Xiao et al. 2017)).

Sensitivity of cat equivalents

We further assess the sensitivity of cat equivalents to strong variation (i.e., 75% variation) in each parameter separately. For a manager it is useful to know in order to choose where to invest resources for monitoring. If a particular parameter has little influence on the cat equivalents, a better resolution of this parameter will change the outcome of cat equivalents only little. We do this by calculating the cat equivalents with the mean estimate of the parameter value and an estimate that was 75% smaller and 75% larger, respectively. This delivers a variation in cat equivalents when a particular parameter is changed and identifies the parameters that have the largest influence on the cat equivalents.

RESULTS

Stressor phase space

Our approach predicts the predator number that is critical for the reproductive success of the population of red-tailed tropicbirds on Christmas Island. We find that, based on the literature estimates of parameter values (Table S1), the red-tailed tropic bird population experiences a stable reproductive success when the system harbors approximately 17 cats in absence of rats or around 1420 rats in absence of cats (intercepts of the border between the red and blue shades in Fig. 2).

The reproductive success is also stable ($\eta = 1$) along this line. When the numbers of cats and rats are above this line, the reproductive success of the bird population is likely negative and the population declines over time (i.e., red shades Fig. 2). In contrast, below the line, the tropicbird population experiences positive reproductive success and an increase over time (i.e., blue shades Fig. 2). A change in the bird population is more likely the further the predator numbers depart from the intercept (represented by stronger color shades (Fig. 2).

By providing an actual critical threshold our conceptual methodology produces an intuitive way of interpreting the total possible threat posed to a species (or system) by multiple stressors. This allows to assess in advance if controlling one stressor might be sufficient to enact the positive changes desired by managers. For the invasive species management on Christmas Island our results imply that the eradication of cats potentially leads to an increase in the tropicbird population if the initial number of rats is below 1420; if it is below 506, the increase is likely (Fig. 2a, medium blue area) and below 97 rats the population of red-tailed tropicbirds is very likely to increase. If, however, the eradication of cats releases rats from predation pressure, cat eradication alone might not be sufficient and might require additional rat control (Fig. 2b). In such a case, it is important to know how many more rats population survive for each removed cat.

Cat equivalents

As for any stressor in a system, we can define one stressor in terms of another as stressor equivalents. Here we present the predation risk of rats in terms of *cat equivalents* - the number of rats that have the same impact on the reproductive success as one cat (Eq. 9, Materials and Methods). The higher this number, the more rats are needed to have the same negative effect on red-tailed tropicbirds as one cat. Cat equivalents can be calculated from the values at the intercept of stable population border (1420 rats divided by 17 cats). This yields a median cat equivalence value of around 80 rats. Thus, cat removal could compromise the survival of the red-tailed tropicbird population if the rat population increased by approximately 80 or more rats per eradicated cat. The uncertainty in this estimate is high, however (68% CI [52, 114] and 95% CI [33, 194]). An increase of more than 114 rats is likely to cause a decline in the bird population and an increase of 194 rats

is highly likely to cause a decline in the bird population.

Parameter sensitivity

Since we found that the cat equivalents are subject to large uncertainty, we investigated which values of parameter estimates contribute most strongly to this. Therefore we assumed a 75% uncertainty around each estimate of a parameter values. Many of the literature estimates of these parameter values show a much better resolution. We found that the metabolic demand of rats, $MetDemand_R$ has the strongest effect on the prediction of cat equivalents. This is to be expected, since the cats equivalents are directly dependent how much a single rat can eat; if they can eat more they are more important. The second most influential parameters are the mass and energy of adult birds $Mass_A$ and $Energy_A$, followed by the physical constraints of cats $MetDemand_C$. Interestingly, the parameters concerning juvenile birds (e.g., μ_J , T_H , $Mass_J$ etc.) seem to have very little effect on the predictions of cat equivalents. Since, the cat equivalents equation Eq. 9 is independent of the parameters A_0 , β and μ_A , we did not assess their sensitivity.

Effects of parameter uncertainty in cat equivalents and critical rats

Parameter uncertainty in our assessment resulted in distributions of cat equivalents and critical rats that are strongly right-skewed with a long tail towards the right hand side, especially the critical rats. Cat equivalents range from 10 to 550, with a median around 80, but with only few scenarios resulting in very large numbers. Critical rat numbers vary widely from 0 to 11000 with a median around 1400.

DISCUSSION

Predicting the outcome of the management of multiple stressors is complicated because systems are complex and information is scarce. The conceptual methodology we presented here, captured available information and energetic limitations to identify critical levels of multiple stressors, and their implications for a management target, while also accounting for different timescales that stressors act on. Our approach estimated critical stressor levels, individually and combined, and the equivalence of one stressor in terms of another. Thereby, we quantified the potential risks of

ignoring the interactions between stressors in a system, and delivered strategic insights into how management actions might bolster the likelihood of success.

For our invasive species example from Christmas Island, we identified three important measures of the system stressors. First, we identified the combined threshold levels of invasive cats and rats under which a population of threatened red-tailed tropicbirds may maintain a desired population trend. Second, we identified the cat equivalents, i.e., how many rats have the same negative effect on the reproductive success of the bird population as a single cat. And third, we demonstrated the number of rats that would put a population of threatened red-tailed tropicbirds at risk of decline when feral cats are being eradicated. With these three stressor estimates, managers can monitor the consequences of cat removal on native species.

The potential of mesopredator release of rats is well documented (Courchamp et al. 1999; Rayner et al. 2007; Prugh et al. 2009) and thus it may appear obvious that an increased number of rats could lead to a decrease in red-tailed tropicbirds after cat eradication. The contribution of our research is to identify (both quantitatively and qualitatively) what increase in the rat population could compromise a species of concern, and thus guide any further resource expenditure requirements. Our method estimates the threshold of rat numbers that, if exceeded, could threaten the population of red-tailed tropicbirds on Christmas Island. Thereby, we identify a quantitative target that can guide rat monitoring after cat eradication. Such monitoring may either occur directly (e.g. as population counts) or indirectly (e.g. observed changes in food resources for rats) depending on the management resources available. This approach supports most effective use of limited resources by informing appropriate timing of both implementing and ceasing rat control activities to keep rat numbers outside the bounds of concern.

Since full eradications are hard to achieve in many ecosystems (Holmes et al. 2015; Holmes et al. 2019), including on Christmas Island, our estimate of stressor equivalence is relevant for two reasons. First, if some cats remain in the system, the population of red-tailed tropicbirds may not be able to cope with the critical rat numbers. For each remaining cat, the critical rats threshold identified by our approach needs to be reduced by the cat equivalents value. Secondly, the cat

equivalents also indicates the increase in rat numbers after cat eradication that the bird population can cope with, before the release of rats becomes a problem.

An important feature of our methodology is that we integrated the information over the relevant timescales in the reproduction indicator. In the case study, rats feed on eggs and chicks, birds take three years to their first breeding, and they breed for about 10 years. An indicator which neglects this time delay could seriously underestimate the impact of rat predation on the bird population. Conversely, cats eat fledglings and adults: an indicator which failed to account for decline in adults would also fail to capture the cumulative impacts of the two stressors in the system. Stressors acting over different timescales is a common phenomenon in environmental systems (O'Brien et al. 2018). Therefore in developing a model to calculate stressor equivalents, it is essential to ensure that the indicator captures the relevant timescales of the different stressors.

The critical stressor levels depend not only on the interaction between the stressors and the timescales involved, but also on the estimates of parameters that are used in the model. Since it is often difficult to obtain system-specific data, our method provides a way of combining literature estimates from other systems and physical constraints. Since we cannot validate the estimates (given the lack of system-specific data), we assessed numerous possible realities by including ranges of estimates of the parameter values. If ranges were not available, we assumed a 20% uncertainty around the mean estimate. This assessment of the uncertainty identified the stressor levels that possibly, likely or highly likely led to a change (positive or negative) in the reproductive success of the red-tailed tropicbirds. Depending on their risk behavior a decision maker can transparently choose a different level of uncertainty.

Assessing the sensitivity of stressor equivalents to model parameters provided important information about where more data can refine model estimates, and which qualitative information could support management decisions. Cat equivalents were mostly driven by physical constraints of rats and cats (metabolic demand and mass). Note that mass is not shown here, as it has the exact same influence on the model as *MetDemand*. The values for metabolic demands derived from a meta-analysis on animal groups (Nagy et al. 1999); specific values from Christmas Island could

therefore change the estimate for cat equivalents considerably. We received estimates for the weight of rats from Christmas Island (personal communication R. Willacy), cat weights were found in the literature (Moseby et al. 2015). Other parameters with a large effect on the cat equivalents, such as the energy in adult birds and eggs and their mass, were obtained from the literature. Despite their potential in a large influence on the cat equivalents, the estimates used in the original assessment exhibited much narrower variation than the 75% in the sensitivity analysis. The proportion of viable eggs was assumed to be quite high in the analysis of the critical stressor levels. A long-term monitoring program on the egg survival rate on Christmas Island could give insights to the managers. Prey preferences showed a varying influence. Since both predators are omnivorous opportunistic feeders, their diet can vary widely with environmental conditions and food availability (Clark 1982; Doherty et al. 2015). Sometimes cats even exhibit individual preferences in their food choice (Konecny 1987). Despite the comparatively little influence of prey preferences on the sensitivity of cat equivalents, habitat-specific diet studies could still narrow down the uncertainty in the cat equivalents.

Environmental systems are often data-poor and subject to cumulative stressors, thus our conceptual methodology is likely to have many applications in other systems with two or more stressors on a management target. While our case study reflected an antagonistic system, our conceptual methodology may be useful for linearly-additive and synergistic stressors as well. Experimental manipulations of microcosm populations have indicated that the interaction between habitat fragmentation and harvesting threatens population size additively (Mora et al. 2007). In additive systems the reduction of one threat does not affect the severity other stressors and should therefore be well described by the here presented stressor equivalents. Since systems with synergistic stressors experience worse effects when cumulative stressors interact, our cumulative stressor level may underpredict the combined stress on the system. However, this is unlikely to be an issue here because we are interested in the effect of a stressor when another is reduced, i.e., the intercepts of the stressor phase space and the stressor equivalents.

Environmental systems are not the only systems affected by cumulative stressors. Socio-

economic systems, medical conditions or mental health problems can all suffer from cumulative interacting stressors (Evans & English 2002; Drimie & Casale 2009; Marcogliese & Pietroock 2011; Pisaniello et al. 2013; Reiss et al. 2019). Children's stress levels, for example, are known to be cumulatively affected by external factors, such as poverty, crowding, noise and substandard housing conditions (Evans & English 2002). In animal health, parasites have been found to interact with natural and anthropogenic stressors increasing mortality and reducing animal health (Marcogliese & Pietroock 2011). Managing complex systems based on single stressors is likely to be ineffective, or worse, have unintended outcomes (Brown et al. 2013). Our conceptual methodology analyses the core stressors of a system and identifies the conditions under which they threaten the system when its being managed. Our approach could prove useful for any system in which multiple stressors threaten a management target.

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- 2 The stressor phase space shows the numbers of cats and rats that may lead to increases (blue shades) or decreases (red shades) in the population of red-tailed tropicbirds. The border between the red and blue shades represents the predator numbers that lead to a stable reproductive success of red-tailed tropicbirds. Departing from stable trajectory are the areas that are included in the 68% credible interval (CI) (medium color shades) and the 95% (darker shades) CI. The arrows represent two management scenarios of cat eradication in stressor phase space. In a) the reduction of cat numbers results in a predator abundance that likely allows the population of red-tailed tropicbirds to increase. In b) cat-only control leads to a substantial increase in rat numbers, so that cat-only management is insufficient for achieving an increasing tropicbird population. 26
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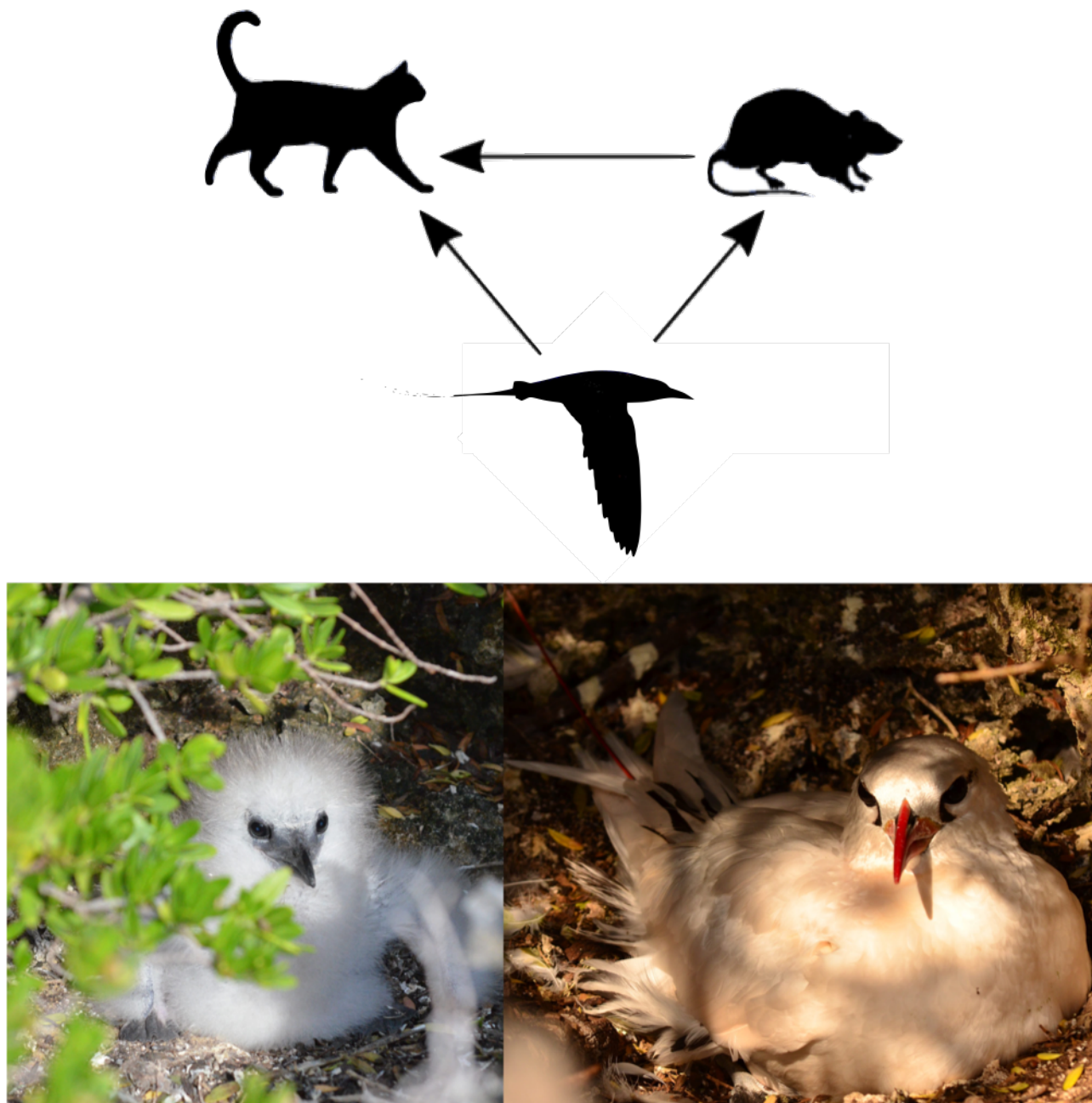


FIG. 1

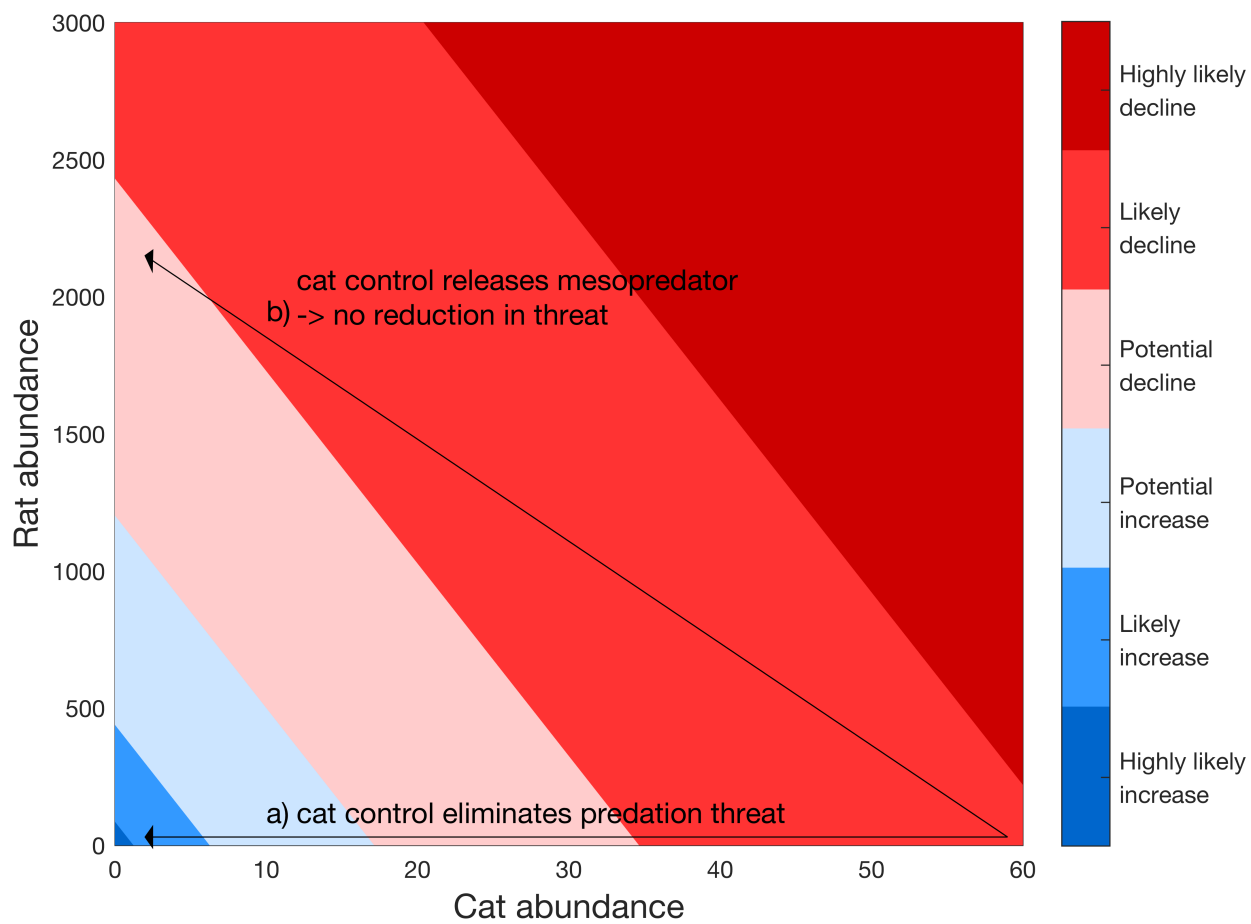


FIG. 2

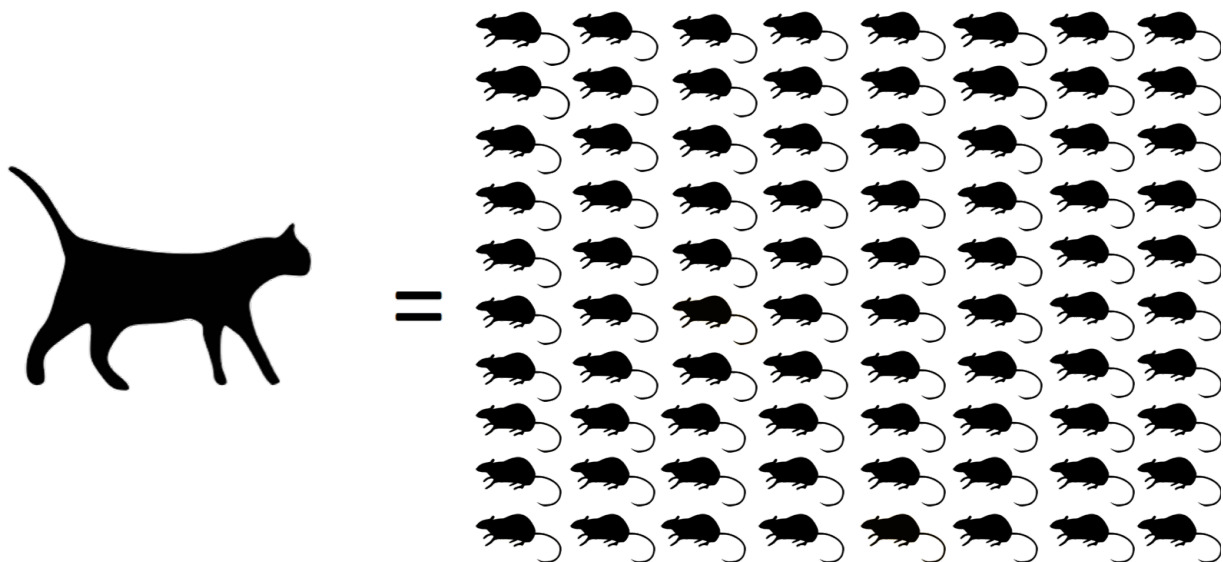


FIG. 3

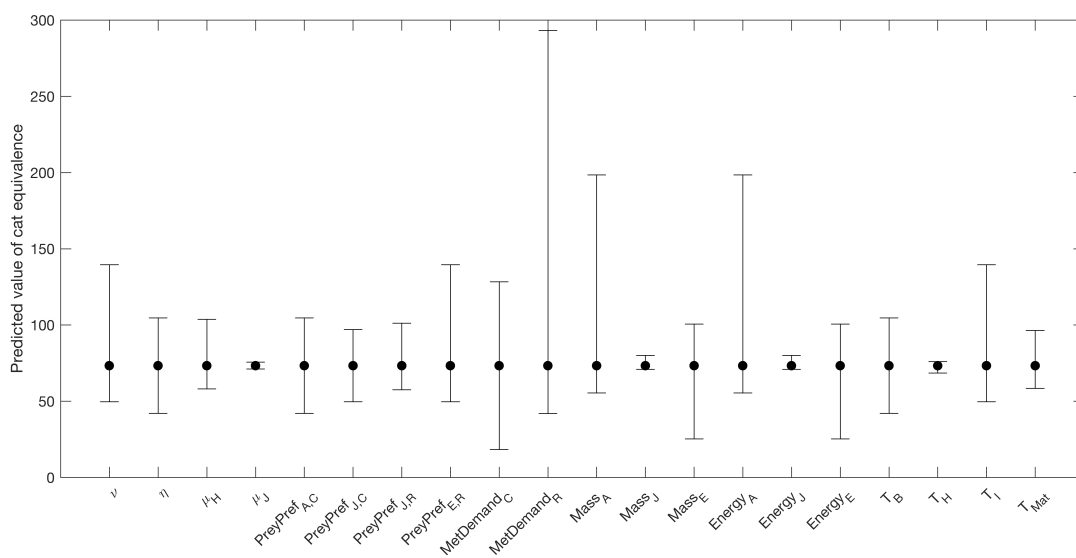


FIG. 4

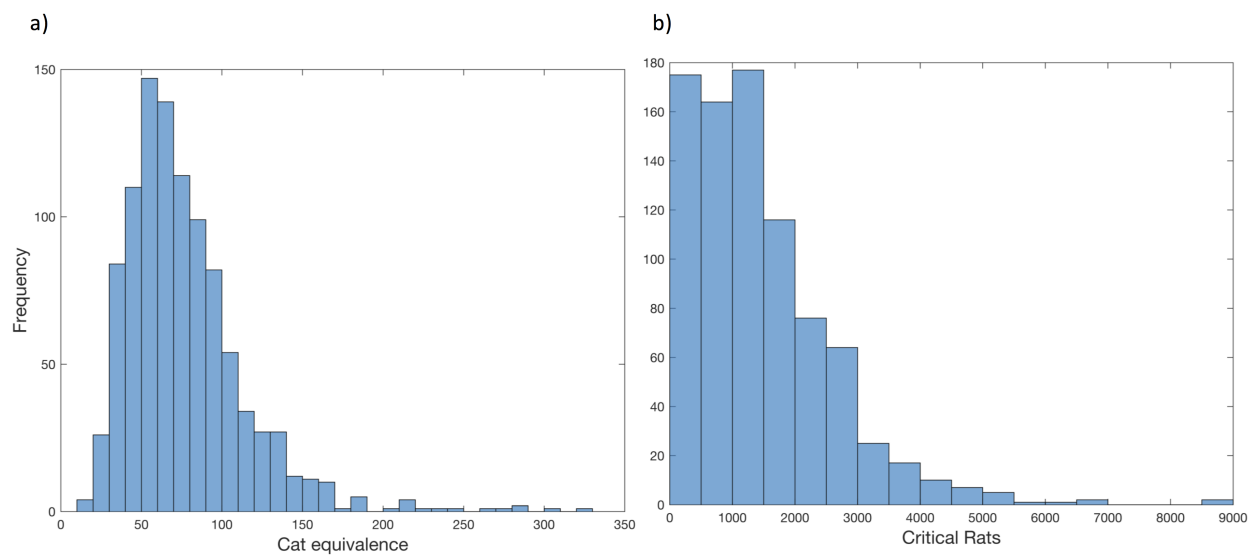


FIG. 5