

Evaluating the use of risk assessment frameworks in the identification of population units for biodiversity conservation

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Abstract

Context. Managing small, isolated populations requires conservation practitioners to weigh up the risks of inbreeding depression and outbreeding depression when assessing alternative management actions aimed at preventing species extinction. Accordingly, it is important that research intended to guide these management decisions provides the relevant evidence to inform them.

Aims. To determine the extent to which studies that use genetic analyses to characterise population units for conservation consider the key theoretical concepts necessary for making sound management recommendations regarding the desirability of gene flow among units, notably the consequences and relative risks of inbreeding depression and outbreeding depression.

Methods. A systematic search was conducted of peer-reviewed literature for studies that attempted to identify population units of threatened birds and mammals. Using content analysis, the theoretical framing of these studies was assessed, based on the discussion of key concepts concerning differences among populations.

Key results. There has been a significant increase over time in the number of published studies that use genetics to identify population units for conservation. Many do not consider theoretical concepts relevant to the effective management of fragmented populations of threatened species. Mammals were more common than birds as focal species of studies, but the number of concepts used in the framing of the studies was similar for these two taxa, despite differences in their ecology and biology that might be expected to affect perceptions of distinctiveness. Nevertheless, species of greater conservation concern tended to have a slightly more comprehensive theoretical framing.

Conclusions. There is great potential for more studies to implement theoretical guidelines and practical decision support tools when considering the best course of action for identifying appropriate population units for conservation management.

Implications. The gap in the identified literature is likely to be impacting the ability of conservation practitioners to make evidence-informed decisions about how to manage the genetic health of threatened species; it would be valuable to improve this situation.

Additional keywords: conservation genetics, conservation management, gene flow, inbreeding depression, outbreeding depression, population units.

Received 1 November 2018, accepted 2 November 2019, published online 8 April 2020

Introduction

Habitat loss and fragmentation have resulted in many species existing in small, isolated populations, increasing their risk of extinction (Frankham *et al.* 2017). Due to their small size and isolation, these fragmented populations often suffer from reduced genetic diversity, inbreeding depression (reduced fitness arising from matings between closely related individuals) and reduced adaptive potential, affecting their probability of persistence and ability to respond to environmental change (Saccheri *et al.* 1998; Weeks *et al.* 2016; Ralls *et al.* 2018). Restoring gene flow among isolated populations can help to alleviate these genetic problems and support population growth, broadly termed genetic rescue

(Pickup and Young 2008; Hedrick and Fredrickson 2010). However, concerns have been raised that restoring gene flow among populations that have become genetically distinct (i.e. gene pool mixing) can lead to outbreeding depression, where offspring have reduced fitness arising from matings between genetically incompatible individuals (Bell *et al.* 2019). In deciding the best course of action for managing small, isolated populations, managers must consider the relative risks of action to restore gene flow (i.e. potential outbreeding depression) versus deciding to manage populations separately (i.e. potential inbreeding depression) when identifying strategies to prevent further declines in biodiversity (Crandall *et al.* 2000).

When assessing the risk of inbreeding depression, it is important to consider to what extent populations are vulnerable to loss of genetic variation, and whether individuals are subject to close inbreeding. Small, isolated populations can lose genetic diversity due to the random process of genetic drift; this can decrease the fitness attainable by individuals in the population and reduce the capacity for adaptation to future conditions (Frankham *et al.* 2017). In such populations, natural selection will be inefficient at removing harmful genetic variants and at promoting beneficial ones, negatively affecting fitness of inbred individuals and suppressing population growth, further accelerating loss of genetic variation and increasing extinction risk (Li 1978; Rich *et al.* 1979; Frankham *et al.* 1999; Pierson *et al.* 2015). Conversely, considering whether populations may be vulnerable to outbreeding depression as a result of gene pool mixing requires consideration of the degree of differentiation among populations, and whether differences between them are likely to be the result of random or adaptive processes (Weeks *et al.* 2016). Populations are more likely to suffer outbreeding depression if their differentiation is adaptive and driven by strong selection pressures, if they are characterised by different co-adapted gene complexes or markedly different chromosomes, or if they have been isolated for many generations (Frankham *et al.* 2011). In the absence of these factors, and when genetic diversity and/or effective population sizes are low, differentiation may simply be the product of random genetic drift, not adaptive, and admixture may entail no negative fitness consequences (Weeks *et al.* 2016).

Given the significant negative consequences for small populations that can accrue from inbreeding depression or outbreeding depression, decision makers managing fragmented populations are faced with difficult choices about how to balance the risks of each. Although managers recognise the value of considering evolutionary processes in management decisions, they often feel that they do not have the expertise to make informed decisions, and rely on advice from experts (Taylor *et al.* 2017; Cook and Sgrò 2018). Yet when populations are small and declining, the negative consequences of inaction perpetuating inbreeding depression may outweigh the harm that could arise from implementing gene pool mixing and risking outbreeding depression (Harrisson *et al.* 2016; Pavlova *et al.* 2017; Ralls *et al.* 2018). In these situations, it is important that managers have the relevant and genetic evidence, or at least the conceptual frameworks, to guide management decisions that have the greatest chance of achieving conservation goals.

There is substantial evidence that shows the negative impacts of inbreeding depression on population persistence can usually be reduced by augmenting gene flow (Frankham 2015; Whiteley *et al.* 2015; Weeks *et al.* 2017). At the same time, the risks of outbreeding depression in many cases may have been overstated and may persist for only a few generations, if at all (Frankham *et al.* 2011; Frankham 2016). Nevertheless, gene pool mixing has rarely been implemented as a management tool, and managers still report concerns about its use (Anthonysamy *et al.* 2018; Bell *et al.* 2019; Cook and Sgrò 2019). Concerns about gene pool mixing are often attributed to a perception that preserving taxonomic integrity and genetic uniqueness is important, along with the risk of disrupting local adaptation and experiencing outbreeding depression (Weeks *et al.* 2016; Love

Stowell *et al.* 2017; Ralls *et al.* 2018; Burrridge 2019). To guide their decisions, managers can benefit from genetic analyses to help assess whether populations should be kept as separate management units or whether they should be actively managed as broader units or metapopulations (Frankham *et al.* 2017). For example, management recommendations to promote gene flow between the critically endangered helmeted honeyeater (*Lichenostomus melanops cassidix*) and its conspecific, the Gippsland yellow-tufted honeyeater (*Lichenostomus melanops gippslandicus*), were informed by characterisation of the origin and extent of genetic differences between the subspecies, application of population viability analysis and demonstration of severe inbreeding depression (Pavlova *et al.* 2014; Harrisson *et al.* 2016, 2019).

Ideally, identifying appropriate management units for conservation actions would be informed by comprehensive information on the fitness consequences of inbreeding and outbreeding. However, such data are rarely available, being typically difficult, expensive and time-consuming to obtain, and thus it is common to use proxies to estimate the risks of fitness consequences of different management scenarios (Frankham *et al.* 2017). The relationships among management units may be informed by an understanding of phenotypic characteristics and environments occupied, along with current genetic population structure and levels of gene flow among populations in the past and more recently (Crandall *et al.* 2000).

We sought to understand whether studies that identify population management units to guide conservation decisions frame their results in relation to the consequences of mixing versus maintaining separate populations, based on the risks of outbreeding depression versus inbreeding depression. Given the importance of decisions about how to manage genetic risks for small populations, we were interested in whether the framing of studies differs based on the conservation status of the focal species, and whether studies made recommendations for population management. The present work provides preliminary insights into the growing number of studies that define population management units to inform conservation decisions about the management of fragmented populations.

Materials and methods

Identifying relevant literature

To assess the theoretical framing of studies that use genetic analyses to identify population units for conservation, we conducted a systematic search of the peer-reviewed literature. We developed a search string to identify relevant literature that: (1) used genetic analyses; (2) defined population units; (3) related to species of conservation concern under state and/or national legislation and/or the IUCN Red List; and (4) included a management objective (Table 1). We focused on studies of mammals and birds because these two groups have well defined taxonomy and are not subject to a diversity of reproductive modes (e.g. selfing and asexuality) or variable ploidy that complicate genetic analyses. Nevertheless, they have different ecology and biology such as different sex biases in dispersal and different dispersal ability, which, coupled with factors such as high levels of interest in plumage differences in birds, could influence the consideration of their population units (Perrin and Mazalov 2000; Sutherland *et al.* 2000; Garnett and Christidis 2017).

Table 1. Search terms used to identify potentially relevant literature

Search terms	Number of records identified	Number of unique records
Initial search strings		
'genetic' AND 'population structure' AND 'endangered'	1296	1081
'genetic' AND 'population structure' AND 'threatened'	771	547
'genetic' AND 'conservation management' AND 'endangered'	277	136
'genetic' AND 'conservation management' AND 'threatened'	145	84
'genetic' AND 'population management' AND 'endangered'	48	36
'genetic' AND 'population management' AND 'threatened'	26	14
'population genetic structure' AND 'endangered'	361	304
'population genetic structure' AND 'threatened'	192	96
'population genetic analysis' AND 'endangered'	31	28
'population genetic analysis' AND 'threatened'	13	10
Search strings added after comparison with training set		
'genetic' AND 'conservation unit*' AND 'endangered'	126	99
'genetic' AND 'conservation unit*' AND 'threatened'	80	46
'genetic' AND 'management unit*' AND 'endangered'	176	109
'genetic' AND 'management unit*' AND 'threatened'	112	75

To evaluate the efficacy of our search terms, we used a training set of articles derived from the 44 relevant mammals and birds included in Pierson *et al.* (2016), who reviewed the inclusion of genetic data and actions in recovery plans for threatened species. These taxa provided a set of species representing conservation management across three continents (Europe, North America and Australia), but were otherwise randomly selected from recovery plans and so provided an external reference point to refine search terms in the present study. The training set included papers for 31 species. Our initial search string did not return papers for all 31 species. Therefore, the final search string included the additional search terms 'conservation unit*' and 'management unit*' (Table 1) to return the full training set. Searches were conducted within Web of Science Core Collection (v.5.29), scanning title, abstracts and keywords for articles published between 1900 and 2018.

Screening potentially relevant articles

The titles and abstracts of all articles returned by the searches were screened to identify studies that: (1) discussed the management of more than one population of a species or subspecies; (2) did not focus on a domestic species; (3) included at least one naturally occurring population (i.e. not exclusively reintroduced or captive-bred populations); (4) used molecular data to analyse population structure; (5) were not concerned solely with basic biology (e.g. natural history) of species and/or populations; and (6) were focused on mammal or bird species. Of the initial 393 articles retained from the screening process, 17 were excluded because they did not meet the initial inclusion criteria when examined on a closer reading during the data collection process, resulting in the 376 papers listed in Table S1, available as Supplementary material to this paper.

Data collection

We conducted a content analysis (a qualitative research method) whereby the full text of articles was searched to identify a predefined set of key themes and ideas (Patton 2002). Articles were coded based on whether they discussed: (1) gene flow;

(2) inbreeding; (3) inbreeding depression; (4) outbreeding; or (5) outbreeding depression (Table 2). Another common term used in the context of outbreeding depression is 'co-adapted gene complexes', so articles that discussed this term were also included within this concept (Templeton 1986) (Table 2). These concepts were targeted because they relate to the fundamental theoretical considerations required to decide whether or not to manage fragmented populations as separate units (Frankham *et al.* 2017). By the nature of the content analysis method, studies recorded for mentioning the term 'inbreeding depression' would include studies that mention the term 'inbreeding', and similarly for 'outbreeding depression' and 'outbreeding'. We also recorded the focal taxon for each study and the year in which the studies were published. We wanted to test whether the level of conservation concern altered approaches to risk assessment and making recommendations. To standardise the threat classification, which can differ among jurisdictions and change over time heterogeneously with respect to taxon, region and date, the 2018 IUCN Red List was used to categorise the threat status of species. Studies were also coded according to whether or not they discussed management recommendations relating to their findings, and whether or not the taxonomic or genetic integrity of the focal taxon was considered, because concerns regarding the integrity or uniqueness of some populations or species are a known barrier to implementing active genetic management (Love Stowell *et al.* 2017). The content analysis was conducted using QSR International's NVivo software (version 10.0.4).

Data analysis

The number of key concepts mentioned within an article was used as a response variable in analyses as an indicator of the complexity of the theoretical framing of a study. A *t*-test was used to assess whether the theoretical framing of studies differed for birds compared with mammals. Linear regression was used to assess whether the theoretical framing of studies varied according to the IUCN threat status of the focal taxon and whether the theoretical framing of studies had changed over time (year of study publication). All statistical analyses

Table 2. The frequency with which relevant concepts were discussed within studies (n = 376)

Key concepts	Number of studies	Proportion of studies (%)
Theoretical framing		
Gene flow ^A	335	89.1
Inbreeding ^A	271	72.1
Inbreeding depression ^A	128	34.0
Inbreeding without inbreeding depression	143	38.0
Outbreeding ^A	67	17.8
Outbreeding depression ^{AB}	55	14.6
Outbreeding without outbreeding depression	12	3.2
Inbreeding and outbreeding	61	16.2
Inbreeding depression and outbreeding depression ^B	37	9.8
Conservation framing		
Discussed management recommendations	194	51.6
Genetic or taxonomic integrity	38	10.1

^AConcepts included in the aggregate score for analyses.

^BStudies using alternative phrase of ‘co-adapted gene complex*’ included in this key concept.

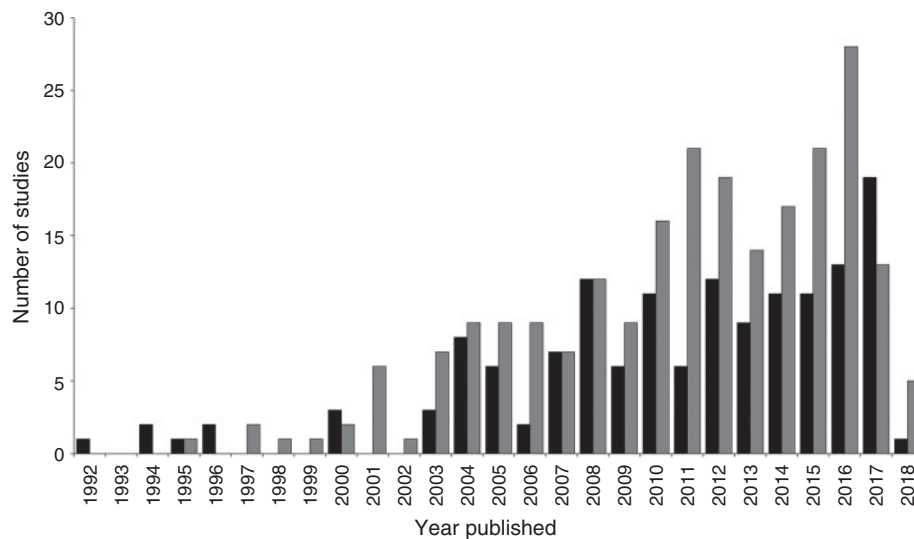


Fig. 1. Number of relevant studies (containing the search terms in Table 1 and meeting the criteria given in Methods) published between 1992 and 2018 for birds (black bars) and mammals (grey bars). The data collection was conducted partway through 2018, which accounts for the low numbers of studies identified for analysis in that year. There will also be some lag in some 2017 papers being available in the literature database used.

were performed in IBM SPSS (version 23) at a significance level of $\alpha = 0.05$.

Results

In total, 2665 unique studies were identified based on the search strings (Table 1), which reduced to 376 after the inclusion criteria were applied (listed in Table S1). The articles were published between 1992 and 2018, with a substantial increase in the number of relevant studies published over time (Fig. 1). There was a taxonomic difference in the number of articles published, with 61% focused on mammals versus 39% on birds; this pattern was maintained or became slightly more pronounced over time (Fig. 1). Most species (35%) were classified as endangered according to the IUCN Red List criteria (Fig. 2).

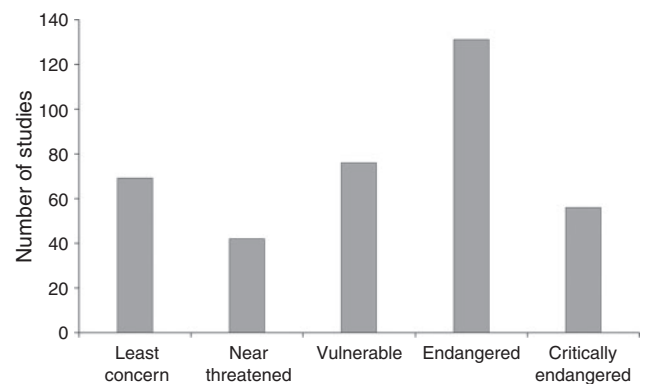


Fig. 2. Number of relevant studies assessing conservation management units based on the conservation status of the target species.

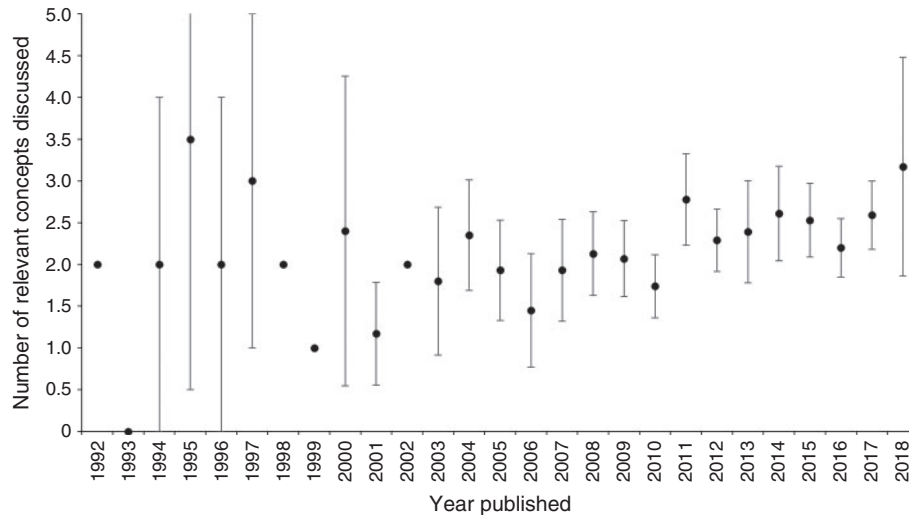


Fig. 3. Mean ($\pm 95\%$ confidence intervals) for the number of relevant concepts discussed in the framing of studies published between 1992 and 2018.

Theoretical framing

On average, articles mentioned 2.3 (± 0.07) of the five terms as part of the theoretical framing for studies defining population management units for threatened species. ‘Gene flow’ was the most frequently discussed concept across the 376 articles (Table 2). ‘Inbreeding’ was also commonly discussed (72% of articles), although the negative fitness consequences of inbreeding – ‘inbreeding depression’ – was mentioned in only 47% of those articles (Table 2). ‘Outbreeding’ was discussed by $\sim 18\%$ of studies. Many of these studies also discussed the negative fitness consequences of outbreeding – ‘outbreeding depression’ (Table 2), with which we also included three additional studies referring to disruption of co-adapted gene complexes (Table 2). Approximately 10% of articles discussed both ‘inbreeding depression’ and ‘outbreeding depression’ within the theoretical framing for their study, and $\sim 16\%$ of studies mentioned both terms of ‘inbreeding’ and ‘outbreeding’ (Table 2). Although a similar number of articles discussed concerns about the impact of gene pool mixing on taxonomic or genetic integrity as part of the relevance of their study for management (Table 2), there was very little overlap between studies considering taxonomic integrity and those considering outbreeding depression ($n = 5$).

There was a weak but significant positive relationship between the number of theoretical terms mentioned and the year of publication ($R^2 = 0.02$, $\beta = 0.035$, $P = 0.006$, Fig. 3), indicating that a wider range of relevant concepts have been included in the theoretical framing over time. The discussion of inbreeding depression and outbreeding depression both increased over time, although the former was approximately twice as common as the latter (Fig. 4). Despite an increase in the number of concepts discussed over time, this effect was small, with year of publication explaining only 2% of variation in theoretical framing.

Although there were more mammal than bird studies published (Fig. 1), similar numbers of theoretical concepts were mentioned for the two taxa ($F_{1,4} = 1.92$, $P = 0.107$). The number of theoretical concepts discussed increased significantly with

increasing Red List status from least concern to critically endangered (Fig. 5), but explained very little of the variation in theoretical framing ($R^2 = 0.02$, $\beta = 0.11$, $P = 0.020$). Despite all species being of conservation concern, and all studies including a management objective, only 52% of articles (birds, 35%; mammals, 65%) discussed the management implication of their results.

Discussion

Our literature-searching process identified 376 peer-reviewed papers published between 1992 and 2018 that used genetic data, defined population units in species of conservation concern with multiple populations and included a management objective. Thus, we consider that these papers were concerned with intraspecific population genetic structure in connection with conservation management.

There was a substantial increase over time in the number of these studies (Fig. 1). The majority of studies mentioned the key concept of gene flow (Table 2). Understanding current and historical levels of gene flow among populations is central to interpreting population genetic structure, and critical in defining meaningfully distinctive segments of species in some frameworks (Crandall *et al.* 2000). However, assessing the implications of managing populations of a threatened species as a single unit or as multiple units also requires consideration of the potential costs and benefits of managing gene flow (Frankham *et al.* 2011; Weeks *et al.* 2011; Ralls *et al.* 2018). Framing decisions in terms of balancing the risks of inbreeding depression and outbreeding depression is necessary when trying to achieve the best outcomes for conservation, but we found that only 10% of the articles we examined used terms that clearly indicated their work was explicitly discussed within this framework (Table 2). Approximately 16% of studies mentioned inbreeding and outbreeding. Even assuming that all of these were concerned with fitness consequences but expressed in terms undetected by our content analysis, a large majority of studies apparently did not consider the relationship between the

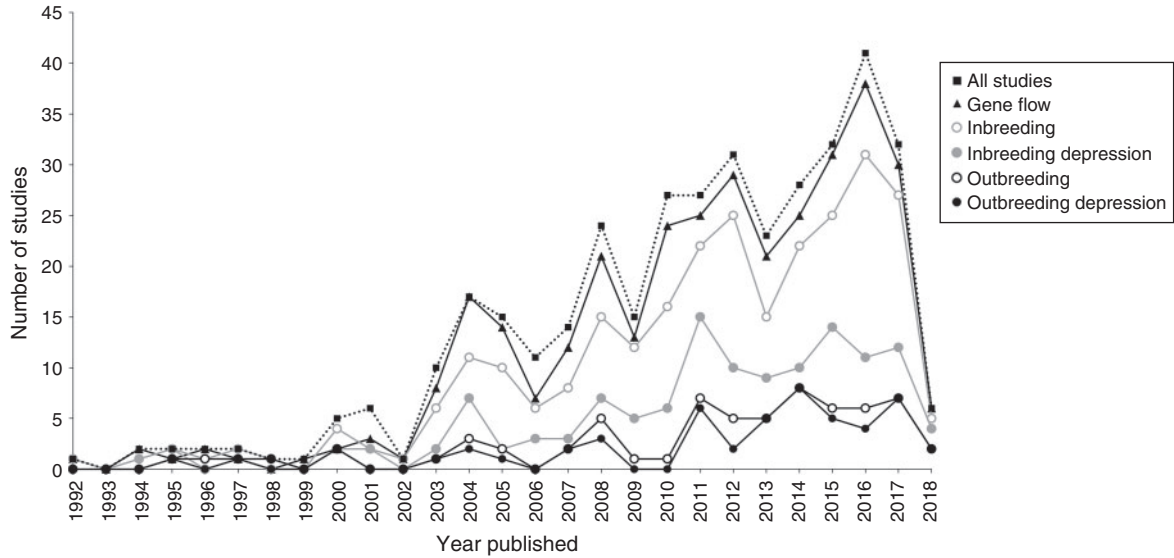


Fig. 4. Number of studies that mention relevant concepts published between 1992 and 2018. Dotted line indicates the total number of studies assessed per year. The data collection was conducted partway through 2018, which accounts for the low numbers of studies identified for analysis in that year. There will also be some lag in some 2017 papers being available in the literature database used.

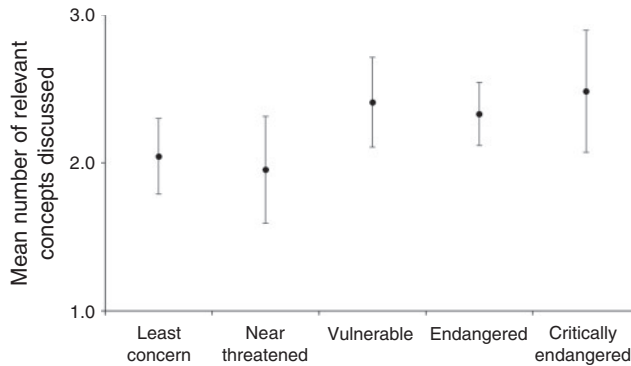


Fig. 5. Mean ($\pm 95\%$ confidence intervals) for the number of relevant concepts discussed in the framing of studies based on the conservation status of the species.

risks of inbreeding depression and outbreeding depression, consistent with the findings of a structured survey in which 318 threatened species recovery plans were read in detail (Pierson *et al.* 2016).

Reference to inbreeding increased over time at a rate similar to all publications, and mentions of inbreeding depression increased at a rate approaching that of overall publications (Table 2; Fig. 4). More than half the studies that mentioned the term inbreeding did not explicitly mention inbreeding depression, the standard term for the harmful effects of inbreeding (Table 2). Although some of this disparity could be a result of alternative terminology and phrasing for inbreeding and inbreeding depression, there is strong evidence to suggest that concepts of genetic fitness have limited profile in conservation management: a study investigating the inclusion of genetic factors in threatened species recovery plans found that only 7% of 318 plans included or planned to collect and include data

on inbreeding, and only 6% for inbreeding depression (Pierson *et al.* 2016).

In addition to this modest level of attention to inbreeding and inbreeding depression, these concepts and their relationship are subject to misunderstanding in the literature. Inbreeding occurs at different levels in the biological hierarchy – within individuals, among individuals within local populations (local population substructure) and among populations. Commonly in the population genetic literature, the single term ‘inbreeding’ is used without clear connection to which of these levels of inbreeding is meant, despite their different biological meanings and implications (Templeton and Read 1994). Most importantly in the current context, ‘inbreeding’ is often used referring to local population substructure (commonly measured by F_{IS} , for example using Weir and Cockerham’s 1984 estimator from molecular data), which in many situations merely reflects genetic heterogeneity associated with the mating system of the species, with little necessary connection to harmful inbreeding. Accordingly, F_{IS} ‘is not recommended as a general measure of inbreeding, as it only reflects deviations from random mating in the most recent generation, rather than total inbreeding over generations’ (Frankham *et al.* 2019: p. 59). Particularly because these concepts are sufficiently nuanced to cause confusion for conservation managers, it is imperative that conservation genetic studies are explicit in their definitions of inbreeding, and present a clear rationale for any inferred connection to fitness and consequent management recommendations (Templeton and Read 1994). Future work will address this issue comprehensively, but a detailed reading of a sample of 16 of the present papers that mentioned ‘inbreeding’ without ‘inbreeding depression’ revealed that only seven made specific reference to negative consequences of inbreeding by some other terms, with the remainder referring to population substructure, often F_{IS} , with no necessary connection to fitness.

Measuring the fitness consequences of inbreeding is far more challenging than estimating the levels of inbreeding (Keller and Waller 2002), so it is unsurprising that many studies defining population units do not quantify inbreeding depression. Nonetheless, this need not preclude consideration of the likelihood and potential consequences of inbreeding depression that could be anticipated from the observed levels of inbreeding, highly relevant when considering managing populations as separate units (Frankham *et al.* 2011; Ralls *et al.* 2018). For example, strong likelihood of inbreeding depression in helmeted honeyeaters (*L. m. cassidix*) was inferred by comparing levels of inbreeding with those in studies of other organisms that had estimated inbreeding depression (Harrisson *et al.* 2016). This assumption was subsequently borne out by quantification of inbreeding depression on lifetime reproductive success (Harrisson *et al.* 2019). Indeed, the relationship between levels of inbreeding and inbreeding depression are sufficiently well quantified in a diversity of organisms that a case has been made that if inbreeding is sufficiently strong, no specific demonstration of inbreeding depression in a given species should be required before considering restorative genetic management actions (Frankham *et al.* 2017; Ralls *et al.* 2018).

The fact that two-thirds of studies in our survey did not mention inbreeding depression, notwithstanding some allowance for alternative forms of expressing the concept, suggests that more attention should be given to the risk posed to population persistence if separate management is recommended for population units (Table 2; Pierson *et al.* 2016). The common practice of managing small, isolated populations without actively managing gene flow can be expected to perpetuate and even accelerate inbreeding depression (Bell *et al.* 2019; Cook and Sgrò 2019). Given the overwhelming evidence linking inbreeding depression with increased extinction probability of small, isolated populations, it is important that the risks of inaction (managing populations in isolation when they could be connected by gene flow) are explicitly considered in decision making (Nieminen *et al.* 2001; Ralls *et al.* 2018; Bell *et al.* 2019). While the number of relevant concepts discussed in the framing of studies we examined has increased slightly over time, the proportion discussing inbreeding depression has increased at most at a similar rate as the overall number of papers defining management units (Fig. 4).

Although many studies did not explicitly discuss the risk from inbreeding depression of managing populations as separate units, there was also limited discussion of risks to populations from treating them as a single management unit, that is, recognising the risk of outbreeding depression (Table 2). The number of papers discussing outbreeding depression has increased over time at most at the same rate as papers overall, and the concept was discussed approximately half as often as inbreeding depression (Fig. 4). Terms to describe outbreeding depression other than those we included (outbreeding depression and co-adapted gene complexes) are sometimes used, but the terms we tested have for many decades been standard ones to describe the negative fitness consequences of outcrossing (Templeton 1986). A low level of consideration of outbreeding depression is consistent with the finding that only 1% of 318 threatened species recovery plans included or planned to include data collection on outbreeding depression (Pierson *et al.* 2016).

In formulating recommendations about genetic management, a key approach is to assess the relative risks of inbreeding depression if populations are maintained in isolation versus the risk of outbreeding depression if gene pool mixing is to be conducted (Weeks *et al.* 2011; Frankham *et al.* 2017; Bell *et al.* 2019). This assessment is important, notwithstanding growing evidence suggesting the risk and persistence of outbreeding depression can be overstated, and that its occurrence is relatively predictable (Frankham *et al.* 2011; Frankham 2016; Bell *et al.* 2019). Where taxonomy is resolved and there are no fixed chromosomal differences, the risk of outbreeding depression should be low (Frankham *et al.* 2011). Even under these circumstances, an explicit acknowledgement that these risks have been considered and deemed unlikely to have negative consequences for populations is appropriate, to demonstrate due diligence and allay any concerns of stakeholders (Cook and Sgrò 2018; Bell *et al.* 2019).

We found evidence for a slight increase in the number of relevant concepts discussed by studies over time, suggesting that theoretical framings may have become more robust (Fig. 3). If so, this may reflect the increased availability of published risk assessment frameworks and decision support tools for assessing whether populations should be managed separately (e.g. Frankham *et al.* 2011; Weeks *et al.* 2011; Ottewill *et al.* 2016; Frankham *et al.* 2017; Ralls *et al.* 2018). We also found some evidence showing that studies focused on species of higher conservation concern tended to have a slightly broader theoretical framing (Fig. 5).

While framing studies in relation to the risks and benefits of actively managing gene flow between populations was uncommon, almost as many studies discussed the implications of their study in relation to maintaining the genetic or taxonomic integrity of populations if they were managed as a single unit (Table 2). There was little (10%) overlap between the studies that discussed outbreeding depression and those that discussed taxonomic integrity, which suggests that considerations around gene pool mixing are focused either on preserving genetic differences or negative fitness concerns, but rarely both. Concerns for maintaining the integrity of a species often prevents the use of gene pool mixing as a tool for improving the genetic condition of small, fragmented populations (Love Stowell *et al.* 2017). Populations that appear to be unique are often prioritised for separate management, due to fears of disrupting local adaptation or diminishing genetic integrity via the introduction of novel genetic variants (Weeks *et al.* 2016). Often, the characteristics of these populations are produced by drift processes, and populations valued for their uniqueness can in fact commonly be those most in need of gene pool mixing to recover fitness (Weeks *et al.* 2016; Frankham *et al.* 2017).

Many studies did not provide any recommendation for management practice, whether based on risks to taxonomic integrity or population persistence (Table 2), despite the conservation relevance of their findings. This may reflect the complexity associated with collecting and interpreting data on genetic population structure, or a tendency to retrospectively frame research in a management context where it was not necessarily an initial motivation of the work. When managers of small, fragmented populations of threatened species are faced

with a situation where even a decision to not take action can have significant consequences for population persistence, any evidence that can inform their assessment of the risks of action versus inaction can have value (Ralls *et al.* 2018). The apparent reticence of researchers to make management recommendations on the basis of their data may contribute to the gap in the consideration of evolutionary and genetic concepts in conservation policies and recovery plans (Pierson *et al.* 2016; Cook and Sgrò 2017). Managers who recognise the value of considering evolutionary processes in management decisions nonetheless often rely on expert advice (Taylor *et al.* 2017; Cook and Sgrò 2018); accordingly, we propose that it would be valuable for researchers to make clear management-relevant interpretations of their data, and ideally offer recommendations with reference to a specified risk assessment framework.

The present study provides insights into how studies are framed in relation to key theoretical concepts relevant to the designation of population units for conservation management. However, we evaluated the literature based on a content analysis of key terms included in papers rather than a nuanced assessment of genetic analyses and interpretation, which might tend to overestimate the degree to which key concepts are being addressed. For example, studies that mention gene flow or inbreeding in relation to conservation units may just be discussing rather than estimating these processes. Likewise, we did not consider whether the genetic analyses used are appropriate to the research question. Given the debate about the most effective way to estimate population structure, and the interpretation of these analyses (Marko and Hart 2011; Jost *et al.* 2018; Milligan *et al.* 2018), there would be great value in understanding whether the genetic analyses used by these studies are appropriate to the research questions being addressed. In particular, it is important to assess how levels of gene flow are estimated by studies that propose population units, and whether conclusions for the management of fragmented populations flow from the data presented. Decisions regarding the management of fragmented populations can be complex and the interpretation highly context-specific. By restricting our analyses to the framing of studies in relation to the risks associated with defining single or multiple units, we focus on the role these studies can play in informing management decisions about how to maximise population persistence.

The results of the present study indicate that discussion of the key concepts relevant to the genetic health and persistence of species of conservation concern could be more thoroughly considered in studies that consider the costs and benefits of gene pool mixing as a conservation management strategy. Evidence-based approaches to management of fragmented populations are required to support the uptake and integration of important evolutionary considerations into conservation management and planning. There is a strong desire by conservation practitioners to use genetic data and include evolutionary considerations in their management (Taylor *et al.* 2017; Cook and Sgrò 2018). However, where studies have an objective of informing threatened species management, there is potential for much greater emphasis on placing findings within a risk assessment framework and making recommendations that could help practitioners identify the best management actions for conservation.

Conflicts of interest

The authors declare no conflicts of interest.

Acknowledgements

We thank the editors of *Wildlife Research* and two anonymous reviewers for their time providing input that improved this paper. Thanks to Jennifer Pierson for providing data for the training set used to validate the search terms used in this study. CNC is supported by an ARC Discovery Early Career Researcher Award. This research did not receive any specific funding.

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