

1 **Balancing conservation and welfare in ex-situ management of the extinct in the wild sihek: sex-**  
2 **and age-specific causes of mortality and contributions to population growth rate**

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19 **Short title:** Conservation and welfare in sihek ex-situ population management

20

21

22 **Abstract**

23 Ex-situ threatened species management has both conservation and welfare objectives and these  
24 objectives often align, but can diverge. Areas of agreement can present win-wins for achieving  
25 welfare and conservation objectives, while identifying areas of divergence is important to ensure  
26 management strategies achieve balance across objectives. We examined welfare and conservation  
27 objectives in the ex-situ population of Extinct in the Wild sihek (Guam kingfisher, *Todiramphus*  
28 *cinnamominus*) by quantifying mortality rates, determining sex- and age-specific causes of mortality  
29 and identifying associated welfare domains, as well as quantifying sex- and age-specific differences  
30 in reproductive value and contributions to variation in population growth rate ( $\lambda$ ). Females had  
31 significantly higher mortality rates than males, potentially impacting population viability and  
32 suggesting females may be more vulnerable to experiencing lower welfare than males. Mitigating  
33 causes of female mortality would therefore present a clear win-win for both welfare and  
34 conservation objectives. Both causes of mortality and contributions to variation in  $\lambda$  were found to  
35 differ across sex- and age-classes. In particular, nutritional and metabolic diseases tended to impact  
36 younger age-classes and these age-classes had large contributions to variation in  $\lambda$ . Mitigation of  
37 these diseases could therefore also present a win-win for welfare and conservation objectives.  
38 However, we also identified a potential divergence between objectives: a major cause of female  
39 mortality was reproductive disease with older aged females primarily affected, but older aged  
40 females contributed little to variation in  $\lambda$  and had low reproductive value. Developing mitigation  
41 strategies for reproductive disease could therefore aid welfare objectives but have little benefit for  
42 conservation objectives, suggesting careful balancing across objectives is required. Our results  
43 highlight the need to explicitly consider conservation and welfare objectives in threatened species  
44 management, in particular in the context of an increasing conservation need for ex-situ population  
45 management, coupled with increasing social concern for animal welfare.

46 **Keywords:** animal conservation; animal welfare; animal health; birth-flow population model; cause  
47 of death; conservation breeding program; Extinct in the Wild

48

## 49 **Introduction**

50 The need for ex-situ management of threatened species is likely to increase across future years as  
51 anthropogenic pressures on wild species and habitats increase (Conde *et al.* 2013; Farhadinia *et al.*  
52 2020). Concurrently, there is increasing social concern for animals and calls for better integration of  
53 animal welfare ethics into conservation management (Beausoleil *et al.* 2018; Alonso, González-  
54 Montaña & Lomillos 2020). In ex-situ population management, conservation and welfare objectives  
55 often agree because individuals with high welfare can have higher survival and reproductive success  
56 than individuals with compromised welfare (Meagher *et al.* 2014; Brown *et al.* 2016). Ex-situ  
57 populations with higher welfare standards may then experience increased population growth rate  
58 ( $\lambda$ ) than populations with lower welfare standards (Clubb *et al.* 2009). Identifying potential areas  
59 where there is scope to improve welfare could then also benefit conservation objectives, and vice  
60 versa (Harrington *et al.*, 2013). However, conservation and welfare objectives in ex-situ management  
61 can occasionally diverge (e.g. translocating animals from the wild to supplement breeding programs,  
62 Kaplan 2022; feeding live prey, Cottle *et al.* 2010), making it difficult for population managers to  
63 identify best management and husbandry strategies (Beausoleil *et al.* 2018). Identifying areas of  
64 agreement or divergence in conservation and welfare objectives is therefore an important step  
65 towards understanding where management action could achieve win-wins for both conservation  
66 and welfare, or where careful balancing across objectives is required to make the best management  
67 decision.

68 Animal welfare ethics recognizes the intrinsic value of animals (Baker 2013) and therefore to achieve  
69 welfare objectives for ex-situ populations, high welfare of all individuals, throughout each animal's  
70 life, is aimed for (Mellor, Hunt, & Gusset, 2015). A commonly used conceptual framework to assess

71 welfare of animals under human care is the Five Domains Model (Mellor & Beausoleil, 2015; Mellor  
72 *et al.*, 2020). This model aims to assess internal and external physiological disturbances due to  
73 nutritional, environmental and health challenges, and to assess the combined anticipated affective  
74 consequences of these challenges on animals' mental states (Mellor, Patterson-Kane, & Stafford,  
75 2009; Mellor & Beausoleil, 2015). Tools to assess an individual's welfare at points during its lifetime  
76 include hormonal assays (e.g. Sheriff *et al.*, 2011) and behavioural markers (e.g. Watters, Krebs, &  
77 Eschmann, 2021). However, carrying out in-depth assessments of every individuals' welfare in a  
78 population, throughout their lifetimes, is not always feasible. In these cases, mortality rates may be  
79 a useful welfare indicator, both because they may provide a broad overview, as opposed to a snap-  
80 shot, of population-level welfare and because mortality data is often routinely collected for ex-situ  
81 populations (e.g. Mason & Veasey, 2010; Thomsen & Houe, 2018; Jaakkola & Willis, 2019). Mortality  
82 rates have been suggested to be low sensitivity welfare indicators because they cannot capture  
83 cases of compromised welfare that do not result in instant death (Hecht 2021) and they assume  
84 death is always preceded by compromised welfare. However, mortality rates have a well-  
85 documented association with welfare in livestock (Thomsen & Houe 2018) and have been found to  
86 correlate with hormonal measures of lifetime stress (e.g. Rakotoniaina *et al.*, 2017). Further,  
87 necropsy or histopathology data can be examined to determine underlying causes of mortality,  
88 which can in turn be linked to associated welfare domains. For example, mortalities due to trauma  
89 can be associated with welfare domain '3: Health', because injury is associated with pain and  
90 distress (Butterworth & Weeks, 2010; Mellor *et al.*, 2020) and may be associated with welfare  
91 domain '4: Behaviour', if injury resulted from negative social interactions (e.g. Foister *et al.*, 2018;  
92 Damme *et al.*, 2022). Quantifying mortality rates and determining causes of mortality in ex-situ  
93 populations can therefore be a useful tool for evaluating broad-scale quality of life of ex-situ  
94 animals, and for identifying management areas where there may be scope to improve welfare.

95 In contrast, species conservation objectives often focus on the collective (i.e. the persistence of  
96 species and ecosystems can take precedence over an individual's needs) and instrumental (i.e. an

97 animal's value comes from its role e.g. in a breeding program) value of animals (Soulé 1985; Wallach  
98 *et al.* 2018). Conservation objectives of threatened species ex-situ population management can  
99 include providing insurance against extinction in the wild (McGowan, Traylor-Holzer & Leus 2017;  
100 Farhadinia *et al.* 2020) and providing a source of individuals for conservation translocations, e.g.  
101 California condor, *Gymnogyps californianus*, USFWS, 2013; Tequila splitfin, *Zoogoneticus tequila*,  
102 Domínguez Domínguez *et al.*, 2018). To achieve their conservation objectives, ex-situ populations of  
103 threatened species often need to be demographically stable, such that they have long-term viability  
104 and can support removal of individuals for releases (Lees & Wilcken 2009; Lacy 2013; Che-Castaldo  
105 *et al.* 2021a). For relatively long-lived species, adult mortality rates are often a key demographic rate  
106 influencing  $\lambda$  (Sæther & Bakke 2000), and thus the ability of ex-situ populations to achieve  
107 conservation objectives. However, causes of mortality may differ across sex- and age-groups  
108 (Lamglait, 2018; Benjamin Lamglait, 2020; Shopland *et al.*, 2020), such that prioritising mitigating  
109 causes of mortality associated with key sex- and age-groups may be required to achieve  
110 conservation objectives. A potential divergence in conservation and welfare objectives could  
111 therefore emerge, where to achieve conservation objectives, management strategies should  
112 prioritise key sex-age classes, whereas to achieve welfare objectives, common causes of death,  
113 regardless of sex- and age-groups impacted, should be prioritised.

114 Sihek (Guam kingfisher, *Todiramphus cinnamominus*) are extinct in the wild (BirdLife International  
115 2017) and therefore are entirely managed ex-situ. Across the sihek ex-situ population, managers aim  
116 to uphold high welfare standards. Alongside this, active species recovery planning is taking place,  
117 which aims to release sihek back to the wild (Laut 2022). The conservation objectives of the ex-situ  
118 population include providing an insurance population against global extinction and supporting  
119 recovery efforts by providing individuals for release. In this study, we examine whether welfare and  
120 conservation objectives in the sihek ex-situ population are in agreement and identify potential areas  
121 of divergence. We first quantify and compare mortality rates of male and female sihek in the ex-situ  
122 population as a broad-scale welfare indicator. We then examine causes of mortality, determine sex-

123 and age-specific differences in causes of mortality, and identify associated welfare domains. Further,  
124 we link this to population processes and conservation objectives by quantifying sex- and age-specific  
125 differences in reproductive value and contributions to variation in  $\lambda$ . If common causes of mortality  
126 impact particular sex- and age-classes that also have large contributions to  $\lambda$ , then mitigation  
127 strategies to reduce these causes of mortality could present win-win scenarios, i.e. welfare and  
128 conservation objectives align, and development of mitigation strategies could be prioritised.  
129 However, if causes of mortality impact sex- and age-classes that have little contribution to  $\lambda$ , then  
130 mitigation strategies could aid welfare objectives but have little benefit towards achieving  
131 conservation objectives. In these cases, welfare and conservation objectives could diverge, meaning  
132 that careful balancing across objectives is required so that best management plans can be  
133 developed.

134

## 135 **Methods**

136 The current sihek ex-situ population is distributed across 26 conservation breeding facilities in the  
137 US mainland and Guam. Management across the population aims to be consistent, with husbandry  
138 practices based on guidelines provided in the sihek husbandry manual (Bahner et al. 1998), however  
139 some differences in management do exist between institutions (e.g. diet provided, enclosure type).  
140 The population is genetically managed using a studbook, with breeding recommendations created to  
141 maintain genetic diversity and to meet the needs of the U.S. Fish and Wildlife Service's species'  
142 recovery program. As such, breeding intensity has varied across the history of the breeding program,  
143 depending on calls to increase or maintain population size (Trask *et al.* 2021).

144 **Review of causes of death** Institutions that are or have been a part of the Guam kingfisher SSP were  
145 solicited for necropsy records (Appendix 1). Records that were incomplete or where a full post-  
146 mortem examination was not performed, as well as unhatched eggs, were removed from analyses.  
147 Studbook data, which has records of exact hatch and death dates for the sihek ex-situ population

148 from 1985 to 2018, was used to calculate age at death. Sihek are sexed based on plumage  
149 dimorphism which occurs from 30 to 45 days post-hatch (Bahner, Baltz & Diebold 1998).  
150 Categorisation and analyses of causes of mortalities were therefore carried out separately for  
151 individuals that died at  $\leq 40$  days post-hatch (hereafter referred to as 'pre-fledglings'), and for  
152 individuals that died at  $>40$  days post-hatch (hereafter referred to as 'adults').

153 Cause of death was classified based on findings recorded in necropsy reports, from gross post-  
154 mortem examinations and/or histopathology. We did not attempt to analyse information on body or  
155 feather condition at death because this information was inconsistently recorded across necropsy  
156 reports. For bacterial diseases, diagnostic techniques recorded as being applied for bacteria  
157 identification are detailed in Appendix 2.4. However, because this review was carried out  
158 retrospectively, differences in criteria used to diagnose bacterial disease as the primary cause of  
159 death, as opposed to being associated with the cause of death, could exist between necropsy  
160 reports. To check consistency of results, a conservative subsample of bacterial disease cases was  
161 created by focusing on mycobacteriosis cases where lesions were explicitly stated as being severe  
162 enough that organ dysfunction was considered likely. Statistical analyses of sex- and age-specific  
163 differences in adult causes of death were then repeated using this conservative subsample  
164 (Appendix 2.4).

165 Causes of death in pre-fledglings and adults were then classified into broad, discrete categories  
166 (Table 1). Category formation was informed by grouping causes of death with aetiologies and by  
167 creating an influence diagram of factors that may influence sihek health, welfare and mortality risk  
168 (Fig. 1). In cases where birds were humanely euthanised, these were categorised based on the  
169 disease process that had led to the need to carry out euthanasia (Appendix 2). The influence  
170 diagram was then extended to map the four physical/functional welfare domains of the Five  
171 Domains Model onto associated cause of death categories (Mellor *et al.* 2009; Mellor & Beausoleil,  
172 2015). Domains 1-3 focus on internal physiological disturbances due to nutritional, environmental

173 and health challenges, respectively, while domain 4 focuses on external physical or biotic conditions  
 174 that may inhibit natural species-typical behaviours. A fifth mental domain can then be assigned  
 175 based on the anticipated consequences of the challenges experienced in domains 1-4 (Mellor *et al.*  
 176 2009; Mellor & Beausoleil, 2015). We did not attempt to assign a fifth mental domain because our  
 177 assessments are based on mortality data, which is assumed to reflect the realised physical  
 178 consequences of compromised welfare, as opposed to anticipated mental consequences. Similarly,  
 179 we do not attempt to assess positive welfare states (Mellor *et al.* 2015) because mortality data is  
 180 commonly linked to welfare compromise. The influence diagram was created with input from sihek  
 181 keepers, managers and veterinarians, with the aim that findings on causes of death could be used to  
 182 identify areas where health and welfare threats require mitigation.

183 Table 1. Categories of different causes of death and their descriptions for pre-fledgling and adult  
 184 sihek in the ex-situ population. *\*Torticollis recorded in adult birds was included in the 'other non-*  
 185 *infectious disease' category.*

Cause of death category	Description
<b><i>Pre-fledglings and adults</i></b>	
Bacterial disease	Disease caused by bacteria is considered the primary cause of death.
Reproductive disease	Disease affecting the mature reproductive system of males and females is considered the primary cause of death.
Trauma	Disease due to traumatic injury caused by a conspecific or heterospecific animal, or by accident or misadventure (i.e. self-trauma) is considered the primary cause of death.
Metabolic/ nutritional disease	Disease due to metabolic and/or nutritional needs not being met is considered the primary cause of death.
Multifactorial	Death due to more than one co-occurring disease process.



Other infectious disease	Disease caused by fungi, viruses, or protozoa as the primary cause of death, or co-infection with bacteria, fungi, viruses, or protozoa as the primary cause of death.
Other non-infectious disease	Disease caused by neoplasia, toxicosis, torticollis, or degenerative joint disease is the primary cause of death.
Iatrogenic	Disease inadvertently caused by medical treatment and/or medical examination, or handling is considered the primary cause of death.
Undetermined	Cause of death could not be determined through necropsy or histopathology.

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***Pre-fledglings only***

Failed yolk internalization	Death due to complications associated with failure of recently hatched chick to absorb yolk sac.
Aspiration	Death due to aspiration of food or yolk material.
Hatch complications	Death due to complications of hatching (e.g. yolk sac rupture, blood loss anaemia, dehydration associated with late hatch, neonatal stress, malposition in ovo).
Torticollis*	Abnormal head and neck position, leading to humane euthanasia.

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187 ***Sex- and age-specific differences in adult causes of death***

188 Our null hypothesis was that all adult cause of death categories could impact male and female sihek  
189 equally across age classes. For reproductive diseases, although specific types of diseases may only  
190 occur in males or females, both sexes have the potential to develop diseases affecting the mature  
191 reproductive system (e.g. testicular and cloacal disorders in male birds, Rosin 2012; Abu-Zahr 2022).

192 The frequency of occurrence of different causes of death were therefore compared between male  
193 and female sihek using  $\chi^2$  tests. Additionally, a relationship between an individual's age at death,  
194 their cause of death and sex, as well as an interaction between cause of death and sex, was  
195 investigated using a generalised linear mixed-effect model (GLMM) with a Poisson error distribution  
196 and with the institution where the individual died included as a random effect. The bobyqa optimizer  
197 was used to assist model convergence by increasing maximum iterations, and models were carried  
198 out in R package 'lme4' (Bates *et al.* 2015). The global model was used to generate a set of models  
199 with all possible combinations of fixed effects, using package 'MuMIn' (Bartoń 2022) and models  
200 were ranked according to Akaike's information criterion, corrected for sample size (AICc). This  
201 suggested that the global model had substantially better fit than models with all other combinations  
202 of fixed effects, therefore model inference was based on the global model (Appendix 2.3). Variance  
203 explained by the model (coefficient of determination,  $R^2$ ) was calculated in R package 'rsq' (Zhang  
204 2021). Post-hoc comparisons for cause of death categories were carried out using R package  
205 'multcomp' (Hothorn *et al.* 2022).

#### 206 ***Sex-specific differences in survival of sihek***

207 Studbook data and Cox proportional hazards regression models were used to explore the effects of  
208 sex on survival probability for sihek in the ex-situ population. The R package 'survival' was used, with  
209 right censored data to include individuals still alive in the population and with individuals clustered  
210 by the institution where they were located at death, or at time of study for censored individuals, to  
211 control for any non-independence between institutions (Therneau 2021). Wild-caught individuals (N  
212 = 29) were removed from this analysis as their hatch date was unknown and individuals that died  
213 before plumage dimorphism, and therefore sexing, occurred (N = 240) were removed, leaving 462  
214 individuals in the dataset.

#### 215 ***Sex- and age-specific differences in reproductive value and contributions to variation in $\lambda$***

216 Matrix population models are often constructed assuming the population follows birth-pulse  
 217 dynamics (i.e. individuals reproduce on or close to their birth-day). However, sihek can breed  
 218 throughout the year in the ex-situ population, with most breeding occurring from December to  
 219 August. Populations that follow birth-pulse dynamics and those that can breed throughout the year  
 220 (i.e. follow 'birth-flow' dynamics) will differ in the distribution of individuals within age classes, and  
 221 therefore different formulae for calculating survival probabilities and fecundities to parameterize the  
 222 population model should be used (Caswell 2018). A two-sex, fully age-structured birth-flow  
 223 projection matrix with a 1-year projection interval was therefore constructed for the sihek ex-situ  
 224 population. Birth-flow survival probabilities ( $P_i$ ) and fecundities ( $F_i$ ) were calculated for each sex- and  
 225 age-class using studbook data, and used to parameterize the population projection matrix,  $A$  (full  
 226 details in Appendix 3).  $A$  consisted of four submatrices to incorporate the contribution of females to  
 227 females ( $A_{ff}$ ), males to females ( $A_{mf}$ ), females to males ( $A_{fm}$ ), and males to males ( $A_{mm}$ ) in the next  
 228 generation, respectively, following Trask *et al.* (2017) and Caswell (2018):

$$229 \quad A = \begin{bmatrix} A_{ff} & A_{mf} \\ A_{fm} & A_{mm} \end{bmatrix}$$

230 The top row of each submatrix was populated with the fecundity terms,  $\frac{1}{2}q(F_i)$ , where  $q$  is the  
 231 primary sex ratio (assumed to be 1:1 male: female, Trask *et al.* 2021) and  $\frac{1}{2}$  is used to account for  
 232 male and female contributions coming each from two submatrices (i.e. to avoid double-counting  
 233 offspring). Sub-diagonal transition probabilities were populated with the calculated  $P_i$  for each sex-  
 234 and age-class. Further details of the projection model structure and parameter values are in  
 235 Appendix 3.

236  $\lambda$  was calculated from the dominant eigenvalue and sex- and age-specific reproductive values from  
 237 the left eigenvector of  $A$ , while elasticities quantified the proportional change in  $\lambda$  due to a  
 238 proportional change in the elements of  $A$  (Caswell 2018). Matrix analyses were carried out using R  
 239 package 'popdemo' (Stott, Hodgson & Townley 2012). 95% confidence intervals around  $\lambda$  and sex-

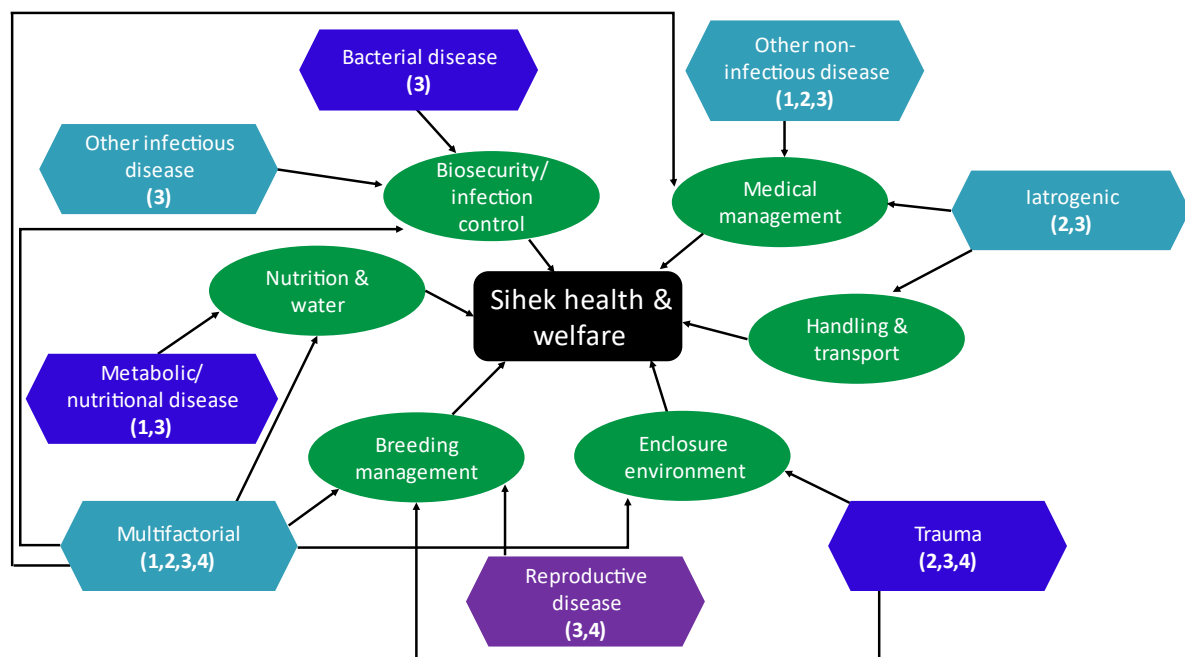
240 and age-specific reproductive values and elasticities were estimated by bootstrap resampling, where  
 241 individuals were randomly resampled with replacement and  $P_i$  and  $F_i$  recalculated, and the matrix  
 242 population model re-fitted to the sample data, with 10,000 iterations. All analyses were carried out  
 243 in program R version 4.1.2 (R Core Team 2021).

244 **Results**

245 **Review of causes of death**

246 We received 299 necropsy reports from adult sihek, constituting 155 females, 143 males and 1  
 247 individual that died at 79 days post-hatch with no sex recorded and which was therefore removed  
 248 from analyses. All four physical/functional welfare domains were associated with at least one of the  
 249 cause of death categories observed in sihek (Fig. 1).

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251

252 *Fig. 1. Influence diagram of different causes of death (hexagons) in the sihek ex-situ population (dark*  
 253 *blue: common, light blue: less common, purple: impacting females only) and associated husbandry or*  
 254 *management areas where potential mitigation strategies could be targeted (green ovals). Numbers*

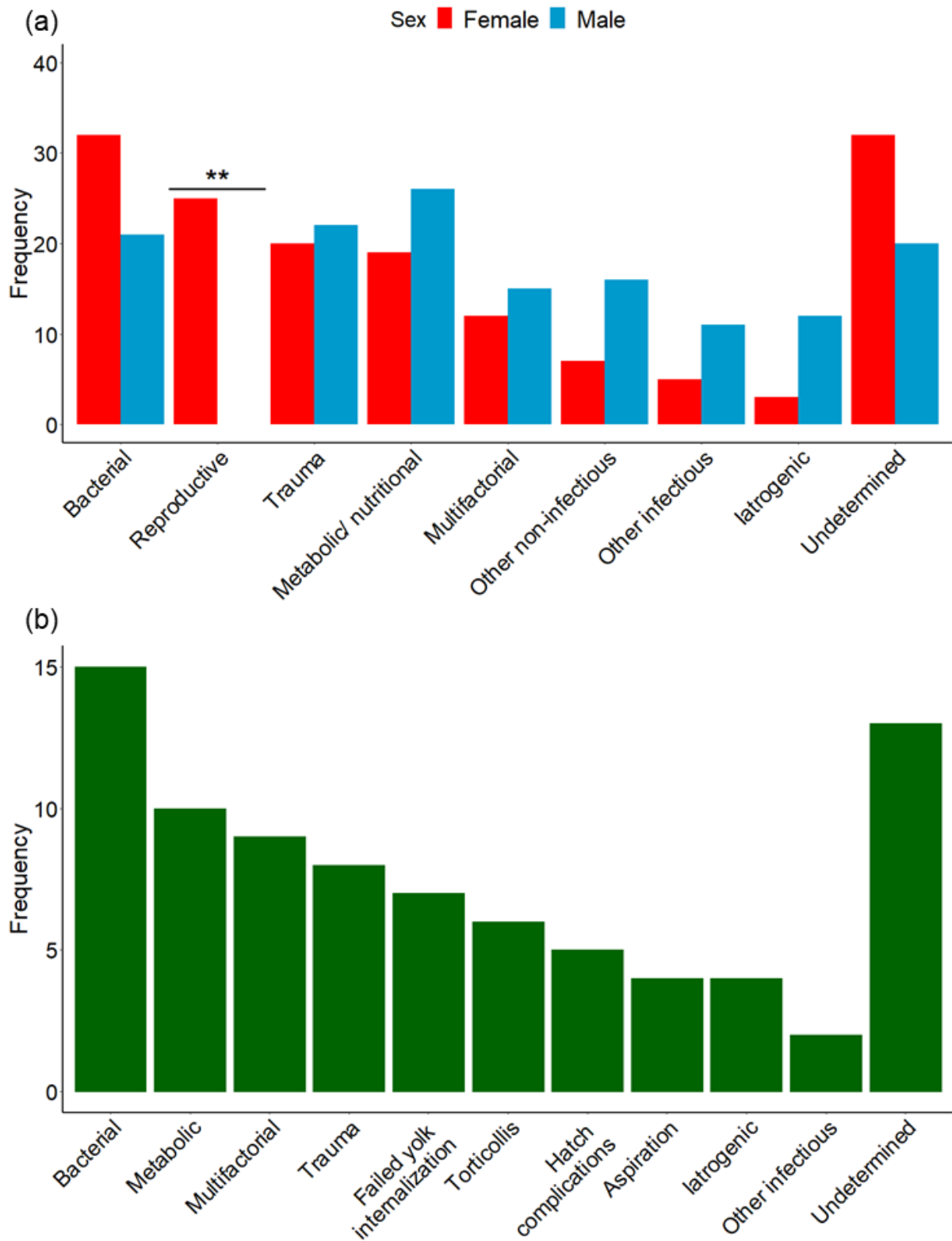
255 *in parentheses indicate associated physical welfare domains (1 = Nutrition, 2 = Environment, 3 =*  
256 *Health, 4 = Behaviour), following Mellor et al. (2009); Mellor & Beausoleil (2015). Causes of death*  
257 *were classed as more common if  $N \geq 31$  and less common if  $N < 30$ , corresponding to the number of*  
258 *cases expected per cause of death category if deaths occurred equally across categories (i.e. 246/8).*

259 Causes of death varied significantly between adult male and female sihek ( $\chi^2 = 42.33$ ,  $df = 8$ ,  $p$   
260  $< 0.001$ ), with this being contributed mainly by a relatively high frequency of deaths from  
261 reproductive disease in females and no deaths associated with the reproductive system observed in  
262 males (Appendix 2.1). In fact, reproductive disease was the second most common cause of death  
263 among adult females (16%, 24/155, Fig. 2a). Excluding 'undetermined' causes of death, the most  
264 common causes of death in adult sihek were from bacterial disease (in particular mycobacteriosis),  
265 metabolic and nutritional diseases, and trauma, with no significant difference in frequency of  
266 occurrence across males and females (Fig. 2a, Appendix 2). Iatrogenic deaths and deaths due to  
267 other non-infectious diseases were more common in males than females, although this was not  
268 significant (Fig. 2a, Appendix 2). Deaths due to other infectious diseases, including fungal, viral and  
269 protozoal diseases, were relatively uncommon in sihek (Fig. 2a, Appendix 2). Deaths due to  
270 multifactorial causes occurred with similar frequency in males and females, with the majority  
271 including metabolic disease as one of the disease processes, but often co-occurring with bacterial or  
272 other infectious diseases (Appendix 2).

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277 Fig. 2. Causes of death of (a) adult sihek by sex and (b) pre-fledging sihek (sexes combined) in the ex-  
 278 situ population. On (a), '\*\*' indicates significant difference at  $P < 0.01$ .

279 We also received 83 necropsy reports from pre-fledgling individuals. The most common causes of  
280 death in pre-fledglings was similar to that in adults (Fig. 2b). However, in the first week post-hatch  
281 causes of death also included hatch complications and failed yolk internalization (further details on  
282 pre-fledgling causes of death are included in Appendix 2.2).

### 283 ***Sex-and age-specific differences in adult causes of death***

284 Age at death was significantly positively associated with reproductive disease (Table 2), with post-  
285 hoc comparisons suggesting a significant difference from age at death associated with bacterial,  
286 metabolic and other non-infectious diseases, and trauma (Appendix 2.3). Causes of death that were  
287 due to bacterial disease, metabolic and nutritional diseases, other infectious diseases, trauma or had  
288 a multifactorial or iatrogenic cause were not significantly associated with age at death (Table 2).  
289 Repeated analyses using a conservative subsample of bacterial disease cases yielded similar results  
290 (Appendix 2.4).

291 Age at death tended to be older for males than females, although this was non-significant (Table 2).  
292 There was a significant interaction between deaths due to metabolic and nutritional diseases and  
293 sex with age at death; males were associated with older age at death while females were associated  
294 with younger age at death from metabolic and nutritional diseases (Table 2, Fig. 1b). There was also  
295 a significant interaction between other non-infectious causes of death and sex with age at death;  
296 males were associated with older age at death while females were associated with younger age at  
297 death from other non-infectious causes (Table 2, Fig. 1b). This was largely driven by neoplasia  
298 causing deaths in older aged males, but no deaths due to neoplasia occurring in females. Iatrogenic  
299 causes of death tended to be associated with younger age at death of males than females, although  
300 this was non-significant (Table 2, Fig. 1b).

301 An interaction between deaths due to reproductive disease and sex with age at death was not able  
302 to be estimated in the model as deaths due to reproductive disease were observed only in females.  
303 To check robustness of our results to the lack of inclusion of the reproductive disease\*sex

304 interaction term, we repeated analyses without the reproductive disease cause of death category  
 305 included, which yielded similar effect size estimates and significance as our full model (Appendix  
 306 2.3).

307 Table 2. Model investigating the relationship between age at death, cause of death and sex.  
 308 Estimated effect sizes, with standard errors in parentheses, and sample size (N) for all fixed effects  
 309 are shown, with the reference level in parentheses. Variance explained by random effects with  
 310 standard deviation in parentheses and variance explained by the model ( $R^2$ ) are also shown.

<b>Fixed effect</b>	<b>Estimate</b>	<b>N</b>	<b>Z</b>	<b>P</b>	<b>R<sup>2</sup></b>
(Intercept)	1.70 (0.09)		19.36	<0.01	0.36
<i>Cause of death category (reference level: Undetermined cause of death category):</i>					
Bacterial disease	-0.20 (0.11)	53	-1.75	0.08	
Iatrogenic	0.22 (0.24)	15	0.91	0.36	
Metabolic disease	-0.08 (0.13)	45	-0.62	0.53	
Multifactorial	-0.10 (0.15)	27	-0.63	0.53	
Other infectious disease	-0.11 (0.22)	16	-0.52	0.60	
<b>Other non-infectious disease</b>	<b>-0.53 (0.22)</b>	<b>23</b>	<b>-2.36</b>	<b>0.02</b>	
<b>Reproductive disease</b>	<b>0.34 (0.11)</b>	<b>25</b>	<b>3.18</b>	<b>&lt;0.01</b>	
Trauma	-0.14 (0.13)	42	-1.11	0.27	
<i>Sex (reference level: Male):</i>	0.19 (0.12)	143	1.67	0.10	
<i>Cause of death category * Sex (reference level: Undetermined cause of death category * Male):</i>					
Bacterial*Sex	0.05 (0.17)	21	0.31	0.75	
Iatrogenic*Sex	-0.52 (0.29)	12	-1.82	0.07	
<b>Metabolic*Sex</b>	<b>0.46 (0.17)</b>	<b>26</b>	<b>2.67</b>	<b>0.01</b>	



Multifactorial*Sex	<0.01 (0.21)	15	0.01	0.99
Other infectious disease*Sex	-0.28 (0.27)	11	-1.04	0.30
<b>Other non-infectious disease*Sex</b>	<b>0.65 (0.25)</b>	<b>16</b>	<b>2.56</b>	<b>0.01</b>
Trauma*Sex	-0.04 (0.18)	22	-0.25	0.80

---

**Random effect**

**Variance**

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Institution	0.03 (0.18)
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311

312 ***Survival of male and female sihek***

313 Male sihek had a significantly greater survival probability than females in the ex-situ population  
314 (Hazard ratio =  $-0.23 \pm 0.09$  SE,  $p < 0.001$ , Fig. 3a). This has resulted in a mean adult lifespan (i.e. for  
315 individuals who reached age 1) of  $5.7 \pm 0.23$  SE and  $7.1 \pm 0.33$  SE and maximum observed lifespan of  
316 15 and 23 years for female and male sihek, respectively.

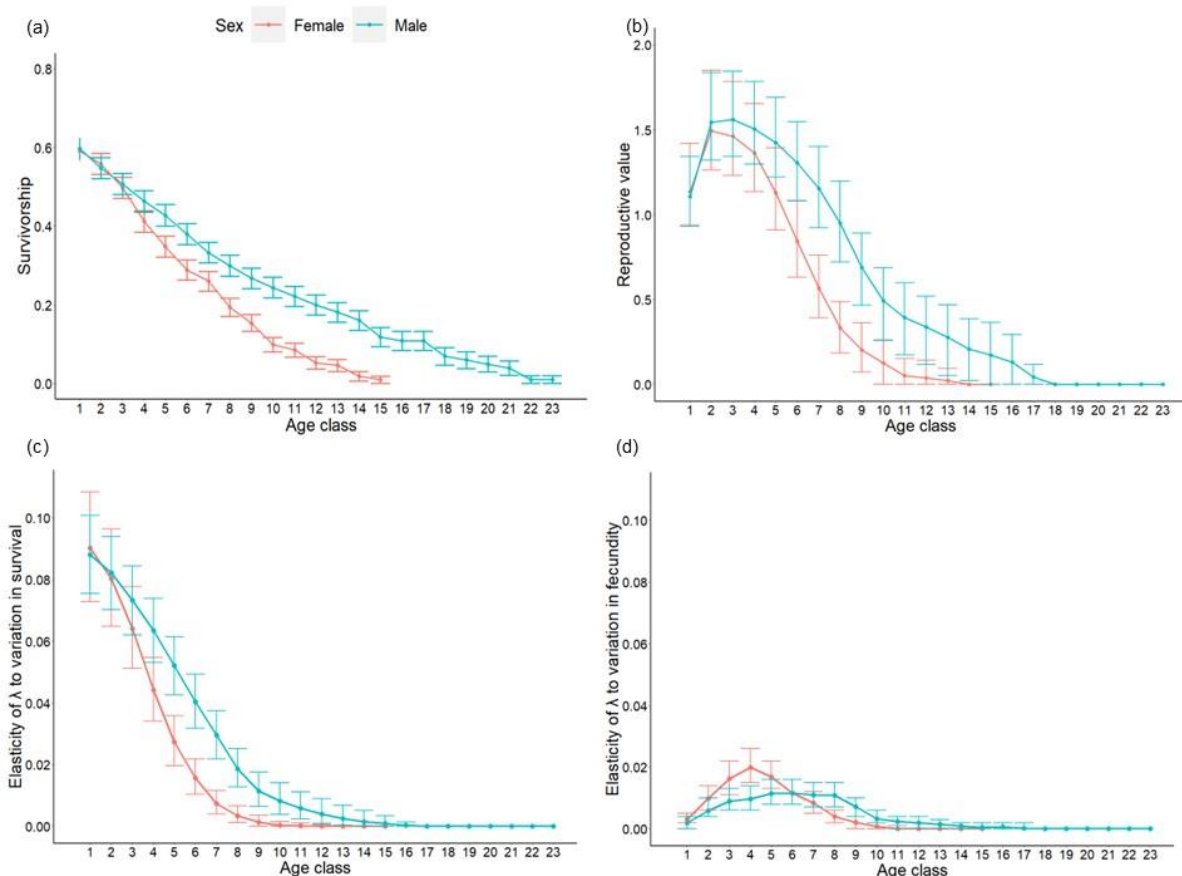
317 ***Sex- and age-specific differences in reproductive value and contributions to variation in  $\lambda$***

318 The population projection model gave  $\lambda = 1.00$  (95% CI: 0.97-1.03). Reproductive values peaked in  
319 age classes 2 and 3, before declining across subsequent age classes. Reproductive values were  
320 similar across sexes in age classes 1 and 2, but showed a relatively rapid decline for females and a  
321 slower decline for males across subsequent age classes (Fig. 3b).

322 Elasticities estimated across sex- and age-specific vital rates suggested that  $\lambda$  was more sensitive to  
323 variation in total adult survival than to variation in juvenile survival or fecundity (total adult survival  
324 = 0.65, total juvenile survival = 0.17, total fecundity = 0.18).  $\lambda$  showed similar sensitivity to variation  
325 in first year survival across sexes (both females and males = 0.09) but was more sensitive to variation  
326 in adult male than adult female survival (males = 0.40, females = 0.24, Fig. 3c). However, when  
327 individual sex- and age-classes were considered, elasticities suggested that  $\lambda$  was more sensitive to  
328 variation in survival of younger than older age classes across sexes.

329 Estimated elasticities for fecundity summed across female versus male age classes suggested that  $\lambda$   
 330 had similar sensitivity to variation in female and male fecundity (total for both female and male  
 331 fecundities = 0.09). However, when considering individual sex- and age-classes, elasticities were  
 332 higher for females in age classes 3-5 than for males in equivalent age classes, but elasticities for  
 333 fecundity of females in subsequent age classes declined sharply and were lower than for fecundity of  
 334 equivalent male age classes (Fig. 3d).

335



336  
 337 *Fig. 3. (a) Probability of survival from hatch to each age class, (b) sex-and age-specific reproductive*  
 338 *values, (c) and (d) elasticities of population growth rate ( $\lambda$ ) to sex- and age-specific survival*  
 339 *probabilities and fecundities, respectively, in the sihek ex-situ population, with standard error bars.*  
 340 *Age classes correspond to individuals aged 0-1 as age class 1, aged 1-2 as age class 2, etc.*

341

## 342 Discussion

343 Sihek ex-situ population management has the joint objectives of achieving and maintaining high  
344 welfare standards for all individual sihek and supporting species conservation. In our study, we used  
345 mortality data and population models to identify where these joint welfare and conservation  
346 objectives may align or diverge in sihek ex-situ population management. We show that many areas  
347 align, presenting potential 'win-win' scenarios if causes of death that affect key sex- and age-groups  
348 for  $\lambda$  can be mitigated. However, we also identify causes of death that primarily impact sex- and age-  
349 groups that contribute little to  $\lambda$ , therefore presenting potential areas of divergence for achieving  
350 conservation and welfare objectives in ex-situ threatened species management.

351 Maintaining high welfare standards is a central objective across ex-situ threatened species  
352 management programs (Mellor *et al.* 2015), and welfare indicators such as mortality rates can be  
353 useful to identify groups vulnerable to compromised welfare (Clubb *et al.*, 2008; Mason & Veasey,  
354 2010; Jaakkola & Willis, 2019). We found that females have a significantly higher mortality rate than  
355 males in the sihek ex-situ population. Although sex-specific survival probabilities of wild sihek are  
356 unknown, this is in contrast to congeneric Pohnpei kingfishers (*T. reichenbachii*), where no significant  
357 differences in wild adult male and female survival probabilities have been observed (Kesler & Haig  
358 2007). Lower adult female versus male survival probability was found in a wild population of  
359 Tuamotu kingfishers (*T. gambieri*) and was suggested to be due to nocturnal predation by invasive  
360 rats on incubating females (Kesler *et al.* 2012), which does not occur in the sihek ex-situ population.  
361 Sex-specific differences in mortality rates have been observed across other ex-situ populations, for  
362 example chimpanzees (*Pan troglodytes*) in American ex-situ populations showed higher adult male  
363 than female mortality, whereas there was no difference in male and female mortality in Japanese  
364 ex-situ populations (Che-Castaldo *et al.* 2021b). Higher adult female than male mortality in the sihek  
365 ex-situ population may indicate that females experience poorer welfare than males, as mortality is

366 assumed to be preceded by negative affective states (Walker *et al.* 2012). Understanding causes of  
367 high female mortality should therefore be a priority to achieve welfare objectives.

368 Once groups at-risk of compromised welfare are identified, determining causes of mortality and  
369 associated welfare domains can then be useful to pinpoint management areas where there may be  
370 scope to improve welfare. In sihek, causes of death varied across sex- and age-classes. Causes of  
371 death have been found to vary across sex and/or age-classes in a variety of taxa in ex-situ  
372 populations, including pink pigeons (*Nesoenas mayeri*, Shopland *et al.* 2020), Struthioniformes  
373 (Lamglait, 2018), Asian elephants (*Elephas maximus*, Jesus, Doherr, & Hildebrandt, 2021) and  
374 springboks (*Antidorcas marsupialis*, Lamglait, 2020), as well as across taxa in the wild (Hill, DeVault &  
375 Belant 2019). A major contributor to the higher female than male mortality rate in sihek was  
376 reproductive disease, with reproductive diseases observed including yolk peritonitis, yolk coelomitis,  
377 egg dystocia and salpingitis. Rates of deaths from reproductive disease in female sihek were  
378 substantially higher than was found in a study of females across a variety of non-domesticated bird  
379 species (Keymer 1980). In particular, occurrences of reproductive disease were associated with  
380 causing death in older-aged female sihek, also in accordance with Keymer (1980). In varanid lizards  
381 in North American zoos, high rate of occurrence of reproductive diseases was suggested to be an  
382 important contributor to higher female than male mortality rates in captive-born but not wild-  
383 caught individuals, potentially linked to husbandry-related issues (Mendyk 2015). Reproductive  
384 disease has been found to be associated with excessive egg production in poultry and commercial  
385 bird species (Keymer 1980; Bowles 2002). High egg production rates could therefore also be  
386 associated with occurrence of reproductive disease in sihek, which in term may increase baseline  
387 female mortality rate and lead to decreased longevity. Further, high reproductive effort has been  
388 found to contribute to increased actuarial senescence rates in birds, which may also contribute to  
389 decreased longevity (Boonekamp *et al.* 2014). A priority step towards achieving welfare objectives  
390 should therefore be to investigate any link between egg production rate, reproductive disease

391 occurrence, and longevity in female sihek, so that underlying causes can be understood, and  
392 mitigation strategies developed.

393 Addressing common causes of death may also aid in achieving welfare objectives, by potentially  
394 improving welfare for the greatest number of individuals (Hecht 2021). The most common cause of  
395 death for female sihek was due to bacterial diseases, with this also being a common cause of death  
396 in males and pre-fledglings. The majority of deaths from bacterial disease in adults were attributed  
397 to mycobacteriosis, with the relatively high frequency of occurrences potentially supporting the  
398 suggestion of a predisposition to hepatic mycobacteriosis in sihek (Gamble 2015). However, because  
399 our review was carried out retrospectively, some differences in criteria used for diagnosis of  
400 mycobacteriosis as the cause of death, as opposed to being associated with cause of death, could  
401 exist between necropsy reports, potentially upwardly biasing frequency of occurrence.  
402 Mycobacterial infection may be due to exposure to infected birds and their environments, or to  
403 environmental sources of saprophytic mycobacteria (e.g. soil, water, Tell, Woods & Cromie 2001).  
404 Depending on the primary disease transmission pathway, recommended infection control strategies  
405 may differ (Witte *et al.* 2021). Further, individual risk factors, such as age at time of exposure, may  
406 play a role in likelihood of disease development (Witte *et al.* 2010). In sihek, identification of primary  
407 disease transmission pathways, as well as individual risk factors for disease development, is  
408 therefore required to design effective infection control measures.

409 To achieve conservation objectives, managers often aim for ex-situ populations to be stable or  
410 increasing in size (Lees & Wilcken 2009; Lacy 2013). In sihek, female-biased mortality has resulted in  
411 a male biased sex ratio developing in the population, with males outnumbering females by age class  
412 four (Newland, Hundgen & Ferrie 2020, Trask *et al.*, 2021). A skewed sex ratio can compromise  
413 population viability by reducing the number of breeding pairs, leading to reduced  $\lambda$ , and reducing  
414 effective population size, leading to increased rate of loss of genetic diversity and increased  
415 inbreeding (Nomura 2002; Wedekind 2002; Grayson *et al.* 2014). As well as being a welfare priority,

416 reducing female sihek mortality rates should therefore also be a conservation priority, to reduce sex  
417 ratio imbalance and aid in achieving long-term population viability.

418 Further, understanding sex- and age-specific contributions to  $\lambda$  can aid in identifying where to focus  
419 management in order to achieve conservation objectives. We found that sihek  $\lambda$  was more sensitive  
420 to variation in total adult survival than juvenile survival or fecundity. This is in agreement with  
421 studies of other long-lived vertebrates (Sæther & Bakke 2000). However, examination of individual  
422 sex- and age-classes suggest that variation in survival of juveniles and fecundity of younger age  
423 adults are important drivers of variation in sihek  $\lambda$ . This importance of demographic contributions  
424 from younger age classes has also been found in wild bird populations (e.g. Reid *et al.* 2004, Schaub  
425 *et al.* 2006, Sim *et al.* 2011). Additionally, younger age classes had higher reproductive value, and  
426 therefore make greater contributions to future generations, than older age classes. In particular,  
427 females reproductive value declined rapidly compared to males across increasing age classes, likely  
428 reflecting the rapidly increasing mortality rate with age in females versus males. To achieve  
429 conservation objectives, strategies to mitigate causes of death that impact younger aged sihek, and  
430 in particular females, such as metabolic and nutritional diseases, should therefore be prioritised. The  
431 most common forms of metabolic and nutritional diseases were liver and renal disease, which may  
432 be linked to nutritional imbalance (Davies 2000; Schmidt 2006). Indeed, obesity has been reported in  
433 the sihek ex-situ population (Slifka, McGill & Oiler 2003). Understanding species' dietary  
434 requirements and ensuring access to balanced diets, in the correct quantities, is therefore key.

435 Meanwhile, strategies to mitigate causes of death that primarily impact sex- and age- classes with  
436 little contribution to variation in  $\lambda$ , such as reproductive diseases that primarily caused death in older  
437 aged females, may be unlikely to aid in achieving conservation objectives. Diseases associated with  
438 causing death in older-aged individuals could have slow progression, such that sub-lethal disease  
439 effects like reduced reproductive success could be apparent in younger-aged individuals, thereby  
440 impacting  $\lambda$ . However, reproductive disease has been associated with high reproductive output

441 (Keymer, 1980; Bowles, 2002), such that expectation may be that female sihek that die from  
442 reproductive disease had high reproductive success when younger. Investigating whether high  
443 reproductive effort is associated with shorter lifespan in sihek, and exploring whether management  
444 strategies such as limiting number of clutches produced by females without impacting  $\lambda$  are  
445 achievable should therefore be priority areas for future study.

446 Taken together, our results reveal areas of alignment between welfare and conservation objectives  
447 in sihek ex-situ population management. In particular, reducing adult female mortality rates would  
448 present a win-win for both welfare and conservation objectives. However, our results reveal  
449 potential divergence between welfare and conservation objectives in how best to achieve  
450 improvements in female sihek mortality rates. Specifically, reproductive disease was found to be a  
451 major contributor to the high female mortality rate, but that older aged females are primarily  
452 affected. From a welfare perspective, causes of reproductive diseases should be addressed,  
453 regardless of age of individuals primarily affected (Mellor *et al.* 2015). However, from a conservation  
454 perspective, decreased occurrence of reproductive diseases may have limited impact on sihek  $\lambda$  and  
455 viability. Instead, addressing causes of death that impact key younger age classes, such as metabolic  
456 and nutritional diseases, may have greater impact in achieving conservation objectives.

457 Our results highlight that  $\lambda$  can differ in sensitivity to variation in different sex- and age-specific  
458 demographic rates, but also that different sex-age classes can differ in their vulnerability to  
459 compromised welfare and in the welfare domains impacted. This can set up the potential for  
460 agreement or divergence in achieving conservation and welfare objectives in population  
461 management. For areas of agreement, these present win-win scenarios (Converse & Sipe 2021), and  
462 therefore should be a priority for management action. However, areas where conservation and  
463 welfare objectives diverge will require careful balancing of alternatives across objectives and values,  
464 for example using a Structured Decision Making framework (Runge *et al.* 2020). Our results  
465 therefore highlight the need to explicitly consider conservation and welfare objectives in threatened

466 species management, and have particular importance against the backdrop of an increasing need for  
467 ex-situ population management, coupled with increasing social concern for animal welfare.

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474 collation.

#### 475 **Author contributions**

476 AT and JE conceived the ideas; AT led the analysis and manuscript writing; CC and RK assisted with  
477 analysis and interpretation of necropsy reports; RM assisted with population modelling analyses; SN,  
478 ER, DF and SM assisted with interpretation of results in relation to husbandry and management  
479 strategies. All authors contributed to manuscript development and gave approval for publication.

480

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667 Fig. 1. Influence diagram of different causes of death (hexagons) in the sihek ex-situ population (dark  
668 blue: common, light blue: less common, purple: impacting females only) and associated husbandry  
669 or management areas where potential mitigation strategies could be targeted (green ovals).  
670 Numbers in parentheses indicate associated physical welfare domains (1 = Nutrition, 2 =  
671 Environment, 3 = Health, 4 = Behaviour), following Mellor *et al.* (2009); Mellor & Beausoleil (2015).

672 Fig. 2. Causes of death of (a) adult sihek by sex and (b) pre-fledging sihek (sexes combined) in the ex-  
673 situ population. On (a), '\*' indicates significant difference at  $P < 0.05$ , '\*\*' indicates significant  
674 difference at  $P < 0.01$ .

675 Fig. 3. (a) Probability of survival from hatch to each age class, (b) sex- and age-specific reproductive  
676 values, (c) and (d) elasticities of population growth rate ( $\lambda$ ) to sex- and age-specific survival  
677 probabilities and fecundities, respectively, in the sihek ex-situ population, with standard error bars.  
678 Age classes correspond to individuals aged 0-1 as age class 1, aged 1-2 as age class 2, etc.

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