

# Does baseline corticosterone influence inter-annual apparent survival of the Thorn-tailed Rayadito?

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## Research

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# Abstract

**Background:** Many studies have attempted to link variation in corticosterone (Cort), the primary glucocorticoid (GC) in birds, with reproductive output, however the consequences of variation in Cort levels on survival probability have been relatively less explored. When considering baseline Cort and survival probability, two hypotheses have been proposed, the cort-fitness hypothesis and the cort-activity hypothesis. Notwithstanding a few exceptions, studies have generally however shown no relationship between levels of baseline Cort and the probability of survival.

**Methods:** With the aim of increasing our understanding of the effect of baseline Cort on survival probability we utilized mark-recapture data from a long-term study (eight years of capture-mark-recapture) of the Thorn-tailed Rayadito (*Aphrastura spinicauda*), fitting different survival models with and without baseline Cort levels as covariates. Secondly, because the two populations in our study have different values of baseline Cort, we evaluated whether the association between baseline Cort and apparent inter-annual survival probability varied in relation to these two populations.

**Results:** In the high latitude population (the population with lower baseline Cort levels), we observed a quadratic (inverted U-shape) relationship between baseline Cort levels and inter-annual survival probability; in the low latitude population, baseline Cort had no apparent effect on inter-annual survival probability.

**Conclusions:** Because of the quadratic relationship, a relationship that only can be observed with long-term data, our approach emphasizes the importance of using a capture-recapture model. In addition, because the effect of baseline Cort on survival probability was found to be context-dependent, our work also highlights the importance of comparing different populations.

## Background

Glucocorticoids (GCs) are essential for life as they regulate or support a variety of important cardiovascular, metabolic, and immunological functions, maintain daily homeostatic energy balance [1], and are involved in the regulation of important life-history trade-offs [2]. GCs are released by the thalamic–pituitary–adrenal cortex (HPA) axis (e.g., [3, 4]). The HPA axis is often divided into two components: baseline glucocorticoid levels and stress response glucocorticoid levels [5]. The first is an approximation of the seasonal baseline level that the animal typically maintains to cope with the predictable demands of its current life history stage [6]. The second, the stress response (the increase in baseline glucocorticoid levels to that reached in 30 min) best reflects short-term plasticity in response to environmental perturbations [7, 8].

Many studies have attempted to link variation in corticosterone (Cort), the primary GC in birds, to reproduction [9, 10, 11, 12, 13, 14, 15, among others], however the consequences of variation in Cort levels on survival (the other component of fitness) have been relatively less explored. Studies that have determined Cort from feathers (Cort<sub>f</sub>: information on total baseline Cort and stress response) have

observed a negative association [16, 17] or no association [18] with survival probability. A similar situation occurs when considering stress response GC levels; some studies have observed a positive association [19], others a negative association [20], or no association at all [21, 22] with return rate or survival probability. When considering baseline Cort two hypotheses have been formulated to describe the relationship between baseline Cort and fitness, the “cort-fitness hypothesis” proposes that individuals with the highest levels of baseline Cort have the worst fitness prospects [23] and the “cort-activity hypothesis”, which argues that elevated levels of baseline glucocorticoids are associated with increased individual fitness through increased locomotory and anti-predator activities [24, 25, 26]. Theory aside, studies of baseline Cort levels generally finds no relationship with survival probability [27] (however two investigations have observed a positive association: [28, 29], two a negative association: [30, 31] and one a quadratic association: [32]). So, with the aim of increasing our understanding of the effect of baseline Cort on survival probability we followed the methodology used by Brown and collaborators [32] and applied the mark-recapture data (e.g., [33]) from a long-term study (eight years of capture-mark-recapture) of the Thorn-tailed Rayadito (*Aphrastura spinicauda*), fitting different survival models with and without Cort levels as covariates. By comparing the fit of survival models with and without covariates, we assessed whether survival varied as a function of a bird’s Cort level and whether it varied in a linear or curvilinear way. Secondly, because in previous studies we had observed that the two populations at the extreme of the species distribution had different values of baseline Cort, both in adults [34] and in nestlings [35], the highest latitude population being the one with lower baseline Cort levels, we evaluated whether the association between baseline Cort and apparent inter-annual survival probability varied in relation to these two populations.

## Methods

### Biology of the Thorn-tailed Rayadito and the study populations

The Thorn-tailed Rayadito (Passeriformes: Furnariidae) is an insectivorous endemic species of the South American temperate forest [36]. Thorn-tailed Rayadito are small (~11 g) and usually lay one clutch per breeding season during the austral spring [37]. Thorn-tailed Rayaditos can live at least nine years (nestlings marked and recaptured nine years later) and their mean the lifespan is 4.8 yr [38]. The nest construction period lasts 6–15 days, and the incubation period is 9–15 days. Eggs are laid on alternate days and the Thorn-tailed Rayadito postpones incubation until after the clutch is complete [37]. As Thorn-tailed Rayaditos are secondary cavity nesters they will adopt artificial boxes, which we monitored, in two populations in Chile over nine reproductive seasons (2008-2017). We monitored 170 nest boxes in Fray Jorge National Park (30°38 S, 71°40 W), the northernmost population (lowest latitude) of the species’ distribution. At this site there is a relic forest composed mainly of Olivillo (*Aextoxicon punctatum*), occurring in patches at the top of the coastal mountain range where fog-induced microclimatic conditions allow the forest to exist in this otherwise semiarid region [39]. In Puerto Williams, on Navarino Island (55°40 S, 67°40 W), which represents the southernmost (and thus highest latitude) limit of the species’ distribution, we monitored 150 nest boxes. At this site, the vegetation is characterized by

deciduous Magellanic forest, whose characteristic species are Lenga Beech (*Nothofagus pumilio*) and Ñirre Beech (*Nothofagus antarctica*).

### **Monitoring, capture procedures and blood sampling**

Hormone levels were sampled in the high latitude population in 2008, 2010 and 2011 and in the low latitude population in 2010 and 2011 [34]. Subsequently, we continuously monitored the populations until 2017. To check for nest box occupation, nest boxes were monitored on a weekly basis. When occupied, the frequency of monitoring was increased in order to detect laying dates (date of first egg) and hatching dates. Adults were captured in their nests between 08:00 and 12:00 with a walk-in trap located in the nest-box entrance hole [37]. For hormone analysis, blood samples (ca. 50  $\mu$ L) were obtained by puncturing the brachial vein with a sterile needle and collecting blood into heparinized micro-hematocrit capillary tubes. In our study, samples were collected within 3 min of capture [34]. Samples were stored on ice until the end of the sampling period (maximum of 5 h) and were then centrifuged for 5 min at 8000 rpm to separate the plasma from red blood cells. The plasma was aspirated with a Hamilton syringe and stored (at -20 °C) until assayed for total CORT content (University of California, Davis). Tarsus length and the weight of each bird were measured. Nestlings and adults were banded with individual metal bands (National Band and Tag Co., Newport, Kentucky, USA and Split Metal Bird Rings, Porzana Ltd, UK) or with a numbered band provided by the Servicio Agrícola y Ganadero (SAG), Chile. This procedure was carried out with the permission of SAG, and the Corporación Nacional Forestal (CONAF), Chile.

CORT levels (i.e., concentrations) in the plasma were determined using direct radioimmunoassays. To determine the efficiency of hormone extraction from the plasma, 20  $\mu$ L of 2000 cpm of tritiated Cort was added to all samples and incubated overnight. Hormones were extracted from the plasma using freshly re-distilled dichloromethane. The aspirated dichloromethane phase was evaporated using a stream of nitrogen at 45 °C. Samples were then reconstituted in phosphate-buffered saline with gelatin. All samples were run in duplicate, and intra-assay variation for Cort ranged from 11.2% to 14.7%, while inter-assay variation was 12.73%. The plasma volumes of the samples varied from 5 to 15  $\mu$ L.

In 2008, baseline Cort was determined from 29 samples in the high latitude populations. In 2010, baseline Cort was determined from 15 samples in the low latitude population and 8 from the high latitude population. In 2011, baseline Cort was determined from 23 samples in the low latitude population and 17 from the high latitude population. In total, 92 blood samples were analyzed, 38 from the low latitude population and 54 from the high latitude population. There were some instances where by chance we obtained samples from the same individual in different breeding seasons (2008, 2010 and 2011). In the present study these duplications have been excluded (five samples collected from the low latitude population and ten samples from the high latitude population). Summarizing, we included 34 bird encounter histories (with accompanying covariate: baseline Cort) (see below) from the low latitude population and 44 bird encounter histories (with its covariate: baseline Cort) from the high latitude population.

## Capture-Mark-Recapture information and analytical procedure

As we had previously observed an absence of differences in baseline Cort levels between males and females [34] together with an absence of difference in survival probability between the sexes [40] we didn't separate capture history by sex (we didn't create two groups) (e.g., [32]). In order to maintain the same number of capture events (i.e., eight reproductive seasons), in the high latitude population we used encounter history from 2008 to 2015 and in the low latitude population from 2010 to 2017. For example, an encounter history of "10000100" indicates that the individual was captured and marked in the first reproductive season, not captured from the second to the fifth reproductive season, captured in the sixth reproductive season and not captured (may be alive or maybe not) in the last two reproductive seasons. In the low latitude population the number of capture-recapture occasions per individual ranged from 1 to 6 (1 = 16, 2 = 7, 3 = 6, 4 = 3, 5 = 1 and 6 = 1), resulting in a total of 71 capture-recaptures of 34 individuals. In the high latitude population the number of capture-recapture occasions per individual ranged from 1 to 8 (1 = 22, 2 = 11, 3 = 5, 4 = 2, 5 = 2, 6 = 1 and 8 = 1), resulting in a total of 91 capture-recaptures of 44 individuals.

To examine the effect of baseline Cort on the probability of survival we applied the Cormack-Jolly-Seber (CJS) model [41] as implemented in MARK software, release 5.1 [42,43]. We used captures to calculate the return rate of birds, which depends on their probability of 1) surviving and coming back to the sampling site ( $\Phi$ , the apparent survival probability) and 2) being encountered ( $p$ , the encounter probability). We generated different models with restrictions on the parameters [33,44]. For example, apparent survival  $\Phi$  (or the rate of recapture  $p$ ) can be restricted in such a way that it can held constant throughout sampling periods – denoted as ( $\bullet$ ), or varied between sampling intervals (1-year interval) - denoted as (t).

We first tested whether our data fitted the full time-dependent CJS model (return rate =  $\Phi(t)p(t)$ ) using the median  $\hat{c}$  estimator provided by MARK to estimate the overdispersion of our data. The  $\hat{c}$  value is used in MARK to adjust the AICc through quasi-likelihood, resulting in a QAICc, whenever  $\hat{c}$  departs from 1.0. This variance inflation adjustment allows the use of data sets that depart from the assumptions of binomial distribution [45]. We based our goodness-of-fit on the CJS model because as yet there are no tractable goodness-of-fit methods available for models with an individual covariate. The approach generally recommended is to perform goodness-of-fit tests based on the more general CJS model and to use the same  $\hat{c}$  value for the models that contain covariates [43]. As the median overdispersion factor ( $\hat{c}$ ) was always inferior to 3, we used CJS models for further analyses. However, when the median  $\hat{c}$  was superior to 1, we multiplied the variance-covariance matrix by the median  $\hat{c}$  to control for the overdispersion of our data. For both populations, the model with the lowest 2nd order Aikake information criteria (AICc or QAICc when the matrix was multiplied by the median  $\hat{c}$ ) was selected as the basic model. For both populations, the null model (return rate =  $\Phi(\bullet)p(\bullet)$ ) (see Results) was the basic model for the subsequent analysis (the lowest AICc or QAICc).

We analyzed the effect of baseline Cort on inter-annual survival by including baseline Cort as a covariate in the basic models and selecting the model with the lowest AICc (or QAICc). Then, we used likelihood ratio tests to determine the significance of the covariates. Some models incorporated Cort as a linear function of survival (denoted:  $C_{\text{Cort}}$ ); others were tested for a curvilinear survival function using the square of Cort as a covariate (denoted:  $C_{\text{Cort-sq}}$ ). MARK automatically standardized all covariates by subtracting the mean from each and dividing by the standard deviation.

## Results

Based on the QAICc, the best model explaining our data in the low latitude population was the model  $\Phi(\bullet)p(\bullet)$  (Table 1). Hence, the apparent survival probability was constant among sampling periods ( $\Phi = 0.65 \pm 0.04$  [0.57–0.73]). With the covariates ( $C_{\text{Cort}}$  and  $C_{\text{Cort-sq}}$ ) included in the model  $\Phi(\bullet)p(\bullet)$ , among year return rate was no best explained by a model including the covariate (Table 2)

Based on the AICc, the best model explaining our data in the high latitude population was the model  $\Phi(\bullet)p(\bullet)$  (Table 3). Hence, the apparent survival probability was constant among periods ( $\Phi = 0.63 \pm 0.04$  [0.54–0.71]). With the covariates ( $C_{\text{Cort}}$  and  $C_{\text{Cort-sq}}$ ) included in the model  $\Phi(\bullet)p(\bullet)$ , among year return rate was best explained by a model including the covariate (Table 4) ( $\Phi(\bullet)_{(C_{\text{Cort}})}(C_{\text{Cort-sq}}) = p(\bullet)$  vs  $\Phi(\bullet) = p(\bullet)$ :  $X^2 = 5.88$ ,  $p = 0.05$ ). Those individuals with intermediate values of basal Cort obtained a higher apparent inter-annual survival rate (Fig. 1).

## Discussion

Our first objective was to evaluate the influence of baseline Cort on inter-annual apparent survival using long-term data. In the high latitude population, we observed a quadratic (inverted U-shape) relationship between baseline Cort levels and inter-annual survival: individuals with baseline Cort near median/average levels had a higher apparent survival probability. To our knowledge the only other investigation that has reported this relationship (quadratic relationship) between baseline Cort and survival probability was undertaken by Brown and collaborators studying Cliff Swallows [32]. This study and our own have in common that both use the mark-recapture model (CJS) (in our study we used a sampling period similar to the life span of the species) and represent the only two studies that have used this approximation (C-M-R methodology including baseline Cort as covariate). Most of the studies which have aimed to evaluate the effect of Cort (baseline Cort or stress response) on survival probability have evaluated the return rate from one single reproductive season to the next [19, 20] or have used a short period of time, i.e. less than one year, or one, two or three years [17, 27, 28, 29, 46]. Short timeframes such as these are disadvantaged in that if an individual is not captured (or seen) during a particular reproductive season, it does not necessarily mean that that individual has died, it may be the individual was just not captured in that particular reproductive season, but, if the captures had continued over more reproductive seasons, the possibility of being recaptured (e.g., 100001001) increases. So we posit that if more studies were to include this approximation (including Cort as a covariate in capture-recapture

models), then it is possible that the quadratic relationship could become more obvious. Moreover, the apparent contradiction between the “cort-fitness hypothesis” and the “cort-activation hypothesis” could be explained by the quadratic relationship (U-shape inverted), “cort-optimal hypothesis” (Fig. 2): that is, when baseline Cort levels are below the optimal (dotted line in Fig. 2) the “cort-activation hypothesis” may be acting (left hand side of Fig. 2), when baseline Cort levels increase above the optimal, the “cort-fitness hypothesis” may be acting (right hand side of Fig. 2). It is interesting to note that a quadratic relationship has also been proposed by Hau and Goymann [47] (but in the context of explaining the relationships between hormone concentration and character expression) and recently Bonier and Cox [48] in a meta-analysis provides some support for the Optimal Endocrine Phenotype Hypothesis. So, the possibility exists that the inverted U-shape we observed reflects both past responses to selection as well as continuous, adaptive adjustment of endocrine phenotypes to track shifting environmental optima, which are often variable among individuals [48].

Why we observed this relationship (inverted U-shape) in the high latitude population, but this was not replicated in the low latitude population, should be investigated in future studies (e.g., Optimal Endocrine Phenotype Hypothesis vs Ongoing Selection Hypothesis sensus [48]). Differences between populations in relation to the influence of Cort on survival has been reported in other studies: Angelier and collaborators observed that stress response Cort levels were positively correlated with return rates in Redstarts that wintered in low suitability habitat (scrub), but not in those that wintered in habitat with a high degree of suitability (mangroves) (no effect of stress response Cort levels on return rates)[19]. So, the individual's environmental context and the phenotypic characteristics are likely to interact and affect fitness (e.g., [12, 49]). In our study the populations differed not only in baseline Cort levels but in several environmental and historical characteristics, the high latitude population presents: (i) lower baseline Cort levels [34 35], (ii) inhabit a quasi-pristine environment, that have no restriction to dispersal [40] and (iii) present higher primary productivity and a more stable environment (lower Coefficient of variation: see Table 1, [34]). The low latitude population presents: (i) higher baseline Cort levels, (ii) inhabits a relict forest isolated from all other Rayadito populations [50] and (iii) the forest is maintained only because of a fog that originates from the nearby ocean [39]. In particular, the intensity of this fog depends on the Humboldt ocean current temperature that in addition determines the El Niño/La Niña events. The dependence of the Fray Jorge National Park with the El Niño/La Niña event has been documented for example in the population dynamics of rodents that ultimately affect raptor population levels [51]. So, the possibility exists that as with other vertebrate species the dynamics of the Rayadito population depend more strongly on abiotic factors (El Niño/La Niña events) rather than physiological characteristics (baseline Cort levels). The influence of el Niño/la Niña events on shaping population dynamics is evident in other vertebrate species: after a weak El Niño event some iguanas died in the Galápagos because of starvation and Romero and Wikelski [22] observed that dead iguanas were typified by a reduced efficacy of negative feedback (i.e. poorer post-stress suppression of Cort release) compared with surviving iguanas, but neither baseline Cort or stress response differed between the dead or live iguanas. So, the possibility exists that in our low latitude population, the efficacy of negative feedback would be the trait that influences survival

probability, so we suggest evaluating the influence of negative feedback on survival probability in future studies.

Finally, as with most capture-mark-recapture studies, two general caveats are in order. One is that we estimate apparent survival only. Those individuals that permanently dispersed out of the study area between sampling periods (between reproductive seasons) would be counted as dead in our analysis (this is the problem with open population models). The other caveat is that hormone levels are not a fixed covariate, they can presumably change for an individual between days or years. The ideal way to analyze survival in relation to hormone level would be to sample the same individuals repeatedly and use a multistate approach [52] in which hormone level represents a covariate that can change among sampling periods, however no statistical method exist for handling varying covariates in multistate models [32].

## **Conclusions**

Baseline Cort is an important trait that affects inter-annual survival probability, however because of the quadratic nature of the relationship, which can only be observed through collection of long-term data, our approach emphasizes the importance of the use of the capture-recapture model. The “cort-optimal-hypothesis”, resolves the apparent contradiction between the cort-fitness hypothesis and the cort-activity hypothesis. Finally, because the effect of baseline Cort on survival probability was observed to be context-dependent, our work also highlights the importance of analyzing and comparing distinct populations.

## **Declarations**

### **Acknowledgements**

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### **Ethical approval**

Ethics approval for this work was obtained from ethics committee of the School of Science, University of Chile, Santiago, Chile. Research was conducted under permit numbers 5193 and 6295 issued by the Servicio Agrícola y Ganadero (SAG), Chile.

### **Authors' contributions**

VQ conceived the idea. VQ collected blood samples, VQ, EBD, EC, PEH and RAV monitored the populations. PGG and JCW analyzed samples. VQ performed statistics and wrote the text. All authors

read and approved the final text.

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## Consent for publication

Not applicable.

## Competing interests

The authors declare that they have no competing interests.

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## References

1. Dallman MF, Strack AM, Akana SF, Bradbury MJ, Hanson ES, Scribner KA, Smith M. Feast and famine: critical role of glucocorticoids with insulin in daily energy flow. *Front Neuroendocrinol.* 1993;14:303–347.
2. Angelier F, Wingfield JC. Importance of the glucocorticoid stress response in a changing world: theory, hypotheses and perspectives. *Gen Comp Endocrinol.* 2013;190:118-28.
3. Sapolsky RM, Romero LM, Munck AU. How do glucocorticoids influence stress-responses? Integrating permissive, suppressive, stimulatory, and adaptive actions. *Endocr Rev.* 2000;21:55–89.

4. Wingfield JC. Control of behavioral strategies for capricious environments. *Anim. Behav.* 2003;66:807–816.
5. Romero LM. Physiological stress in ecology: lessons from biomedical research. *Trends Ecol Evol.* 2004;19:249–255.
6. Landys MM, Ramenofsky M, Wingfield JC. Actions of glucocorticoids at a seasonal baseline as compared to stress-related levels in the regulation of periodic life processes. *Gen Comp Endocrinol.* 2006;148:132–149.
7. Romero LM. Seasonal changes in plasma glucocorticoid concentrations in free-living vertebrates. *Gen Comp Endocrinol.* 2002;128:1–24.
8. Wingfield JC. Ecological processes and the ecology of stress: the impacts of abiotic *Func Ecol.* 2013;27:37-44
9. Bauch C, Riechert J, Verhulst S, Becker PH. Telomere length reflects reproductive effort indicated by corticosterone levels in a long-lived seabird. *Mol Ecol.* 2016;25:5785-5794.
10. Bonier F, Moore IT, Robertson RJ. The stress of parenthood? Increased glucocorticoids in birds with experimentally enlarged broods. *Biol Lett.* 2011;7:944–946.
11. Love OP, Breuner CW, Vézina F, Williams TD. Mediation of a corticosterone-induced reproductive conflict. *Horm Behav.* 2004;46:59–65.
12. Madliger CL, Love OP. Do baseline glucocorticoids simultaneously represent fitness and environmental quality in a declining aerial insectivore?. *Oikos* 2016;125:1824-1837.
13. Ouyang JQ, Sharp PJ, Dawson A, Quetting M, Hau M. Hormone levels predict individual differences in reproductive success in a passerine bird. *Proc Roy Soc B.* 2011;278:2537–2545.
14. Schoenle LA, Dudek AM, Moore IT, Bonier F. Red-winged blackbirds (*Agelaius phoeniceus*) with higher baseline glucocorticoids also invest less in incubation and clutch mass. *Horm Behav.* 2017;90:1-7.
15. Williams CT, Kitaysky AS, Kettle AB, Buck CL. Corticosterone levels of tufted puffins vary with breeding stage, body condition index, and reproductive performance. *Gen Comp Endoc.* 2008;158:29–35.
16. Harms NJ, Legagneux P, Gilchrist HG, Bêty J, Love OP, Forbes MR, Bortolotti GR, Soos C. Feather corticosterone reveals effect of moulting conditions in the autumn on subsequent reproductive output and survival in an Arctic migratory bird. *Proc Roy Soc B.* 2015;282:20142085.
17. Koren L, Nakagawa S, Burke T, Soma KK, Wynne-Edwards KE, Geffen E. Non-breeding feather concentrations of testosterone, corticosterone and cortisol are associated with subsequent survival in wild house sparrows. *Proc Roy Soc B.* 2011;279:1560-1566.
18. Crossin GT, Phillips RA, Lattin CR, Romero LM, Williams TD. Corticosterone mediated costs of reproduction link current to future breeding. *Gen Comp Endocrin.* 2013;193:112–120.
19. Angelier F, Holberton RL, Marra P.P. Does stress response predict return rate in a migratory bird species? A study of American redstarts and their non-breeding habitat. *Proc Roy Soc B.* 2009;276:3545-3551.

20. MacDougall-Shackleton SA, Dindia L, Newman AEM, Potvin DA, Stewart KA, MacDougall-Shackleton EA. Stress, song and survival in sparrows. *Biol Lett.* 2009;5:746-748.
21. Ouyang JQ, Sharp P, Quetting M, Hau M. Endocrine phenotype, reproductive success and survival in the great tit, *Parus major*. *J Evol Biol.* 2013;26:1988–1998.
22. Romero LM, Wikelski M. Stress physiology as a predictor of survival in Galapagos marine iguanas. *Proc Roy Soc B.* 2010;277:3157-3162.
23. Bonier F, Martin PR, Moore IT, Wingfield JC. Do baseline glucocorticoids predict fitness? *Trends Ecol Evol.* 2009;24:634–642.
24. Breuner CW, Hahn TP. Integrating stress physiology, environmental change, and behavior in free-living sparrows. *Horm Behav.* 2003;43:115–123.
25. Comendant T, Sinervo B, Svensson EI, Wingfield J. Social competition, corticosterone, and survival in female lizard morphs. *J Evol Biol.* 2003;16:948–955.
26. Cote J, Clobert J, Meylan S, Fitze PS. Experimental enhancement of corticosterone levels positively affects subsequent male survival. *Horm Behav.* 2006;49:320–327.
27. Jimeno B, Briga M, Hau M, Verhulst S. Male but not female zebra finches with high plasma corticosterone have lower survival. *Func Ecol.* 2018;32:713-21.
28. Cabezas S, Blas J, Marchant TA, Moreno S. Physiological stress levels predict survival probabilities in wild rabbits. *Horm Behav.* 2007;51:313-320.
29. Rivers JW, Liebl AL, Owen JC, Martin LB, Betts MG. Baseline corticosterone is positively related to juvenile survival in a migrant passerine bird. *Func Ecol.* 2012;26:1127-1134.
30. Kitaysky AS, Piatt JF, Wingfield JC. Stress hormones link food availability and population processes in seabirds. *Mar Ecol Prog Ser.* 2007;352:245-258.
31. Kitaysky AS, Piatt JF, Hatch SA, Kitaiskaia EV, Benowitz-Fredericks ZM, Shultz MT, Wingfield JC. Food availability and population processes: severity of nutritional stress during reproduction predicts survival of long-lived seabirds. *Func Ecol.* 2010;24:625-637.
32. Brown CR, Brown MB, Raouf SA, Smith LC, Wingfield JC. Effects of endogenous steroid hormone levels on annual survival in cliff swallows. *Ecology* 2005;86:1034-1046.
33. Lebreton JD, Burnham KP, Clobert J, Anderson RA. Modelling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecol Monog.* 1992;62:67-118.
34. Quirici V, Venegas CI, González-Gómez PL, Castaño-Villa GJ, Wingfield JC, Vásquez RA. Baseline corticosterone and stress response in the Thorn-tailed Rayadito (*Aphrastura spinicauda*) along a latitudinal gradient. *Gen Comp Endocrinol.* 2014;198:39-46.
35. Quirici V, Guerrero CJ, Krause JS, Wingfield JC, Vásquez RA. The relationship of telomere length to baseline corticosterone levels in nestlings of an altricial passerine bird in natural populations. *Front Zool.* 2016;13:1-7.

36. Remsen JV. Family Furnariidae (ovenbirds). In: del Hoyo J, Elliott A, Christie DA. (Eds.), Handbook of the Birds of the World. Broadbills to Tapaculos. 2003; vol. 8. Lynx Edicions, Barcelona, pp. 162–357.
37. Moreno J, Merino S, Vásquez RA, Armesto JJ. Breeding biology of the Thorn-tailed Rayadito (Furnariidae) in south-temperate rainforests of Chile. *Condor* 2005;107:69–77.
38. Quirici V, Hammers M, Botero-Delgadillo E, Cuevas E, Espíndola-Hernández P, Vásquez RA. Age and terminal reproductive attempt influence laying date in the thorn-tailed rayadito. *J Avian Biol* 2019;<https://doi.org/10.1111/jav.02059>
39. Villagrán C, Armesto JJ, Hinojosa LF, Cuvertino J, Pérez C, Medina C. El enigmático origen del bosque relicto de Fray Jorge. In: Squeo, F.A., Gutiérrez, J.R., Hernández, I.R. (Eds.), *Historia Natural del Parque Nacional Bosque Fray Jorge*. Universidad de La Serena Editions, La Serena, Chile. 2004. pp. 173–185.
40. Botero-Delgadillo E, Quirici V, Poblete Y, Cuevas E, Kuhn S, Girg A, Teltscher K, Poulin E, Kempenaers B, Vásquez RA. Variation in fine-scale genetic structure and local dispersal patterns between peripheral populations of a South American passerine bird. *Ecol Evol*. 2017;7:8363–8378.
41. Sandercock BK. Estimation of survival rates for wader populations: a review of mark-recapture methods. *Wader Study Group Bull* 2003;100:163-174.
42. White GC, Burnham KP. Program MARK: survival estimation from populations of marked animals. *Bird Study* 1999;46:120-138.
43. Cooch E, White G. Program Mark: a gentle introduction. 2008; 7th edition. <http://www.phidot.org/software/mark/index.html>
44. Nichols JD. Capture-recapture models. Using marked animals to study population dynamics. *Bioscience* 1992;42:94-102.
45. Burnham KP, Anderson DR. Model selection and inference: a practical information-theoretic approach. 2002. Second edition. Springer-Verlag, New York, New York, USA.
46. Goutte A, Angelier F, Welcker J, Moe B, Clément-Chastel C, Gabrielsen GW, Chastel O. Long-term survival effect of corticosterone manipulation in black-legged kittiwakes. *Gen Comp Endocrinol*. 2010;167:246-251.
47. Hau M, Goymann W. Endocrine mechanisms, behavioral phenotypes and plasticity: known relationships and open questions. *Front. Zool*. 2015;2(S1), S7.
48. Bonier F, Cox RM. Do hormone manipulations reduce fitness? A meta-analytic test of the Optimal Endocrine Phenotype Hypothesis. *Mol Cell Endocrinol*. 2019. 110640.
49. Vitousek MN, Johnson MA, Downs CJ, Miller ET, Martin LB, Francis CD, Husak JF. Macroevolutionary patterning in glucocorticoids suggests different selective pressures shape baseline and stress-induced levels. *Am Nat*. 2019;193:866-880.
50. Yáñez DI, Quirici V, Castaño-Villa GJ, Poulin E, Vásquez RA. Isolation and characterisation of eight microsatellite markers of the thorn-tailed rayadito *Aphrastura spinicauda*. *Ardeola*. 2015;62:179–83.
51. Lima M, Keymer JE, Jaksic FM. El Niño–Southern Oscillation–driven rainfall variability and delayed density dependence cause rodent outbreaks in western South America: Linking demography and

population dynamics. *Amer Naturalist*. 1992;15:476-491.

52. Lebreton JD, Nichols JD, Barker RJ, Pradel R, Spendelov JA. Modeling individual animal histories with multistate capture–recapture models. *Adv Ecol Research* 2009;41:87-173.

## Tables

**Table 1**

Model selection testing for the effect of period interval on the return rate of the Thorn-tailed Rayadito in the low latitude population.

Model	QAICc	Delta QAICc	AICc Weights	Model Likelihood	Num. Par	QDeviance
$\Phi(\bullet) = p(\bullet)$	138.50	0.00	0.46	1.00	1.00	44.34
$\Phi(t) = p(t)$	140.17	1.67	0.20	0.43	7.00	32.21
$\Phi(\bullet) \neq p(\bullet)$	140.29	1.80	0.19	0.41	2.00	44.01
$\Phi(\bullet) = p(t)$	140.91	2.41	0.14	0.30	8.00	30.36
$\Phi(t) = p(\bullet)$	146.65	8.16	0.01	0.02	8.00	36.11
$\Phi(t) \neq p(t)$	151.69	13.19	0.00	0.00	14.00	23.67

Notes: Mean  $\hat{c} = 1.12$ . Time dependence is indicated with (t); constant over time is indicated with ( $\bullet$ ).

**Table 2**

Model selection testing for the effect of baseline Cort on the return rate of the Thorn-tailed Rayadito in the low latitude population.

Model	QAICc	Delta QAICc	AICc Weights	Model Likelihood	Num. Par	QDeviance
$\Phi(\bullet) = p(\bullet)$	138.50	0.00	0.28	1.00	1	136.44
$\Phi(t) = p(t)$	140.17	1.67	0.12	0.43	7	124.31
$\Phi(\bullet)_{(Cort)} = p(\bullet)$	140.61	2.11	0.10	0.35	2	136.43
$\Phi(\bullet)_{(Cort)} (Cort-sq) = p(\bullet)$	140.96	2.46	0.08	0.29	3	134.58
$\Phi(t) \neq p(\bullet)$	146.65	8.16	0.00	0.02	8	128.21
$\Phi(t) \neq p(t)$	151.69	13.19	0.00	0.00	14	115.77

Notes: Mean  $\hat{c} = 1.12$ . Time dependence is indicated with (t); constant over time is indicated with ( $\bullet$ ). In some models, corticosterone ( $_{(Cort)}$ ) alone or combined with its square (Cort-sq) were linear or curvilinear covariates respectively; those without these subscripts had no effect of corticosterone.

### Table 3

Model selection testing for the effect of period interval on the return rate of the Thorn-tailed Rayadito in the high latitude population.

Model	AICc	Delta AICc	AICc Weights	Model Likelihood	Num. Par	Deviance
$\Phi(\bullet) = p(\bullet)$	168.193	0	0.52	1	1	64.72
$\Phi(\bullet) \neq p(\bullet)$	168.72	0.52	0.39	0.77	2	63.14
$\Phi(t) p(\bullet)$	172.13	3.93	0.07	0.14	8	52.85
$\Phi(t) = p(t)$	175.67	7.48	0.01	0.02	7	58.83
$\Phi(\bullet) \neq p(t)$	180.11	11.92	0.00	0.00	8	60.84
$\Phi(t) \neq p(t)$	182.89	14.71	0.00	0.00	13	50.48

Notes: time dependence is indicated with (t); constant over time is indicated with ( $\bullet$ ).

**Table 4**

Model selection testing for the effect of baseline Cort on the return rate of the Thorn-tailed Rayadito in the high latitude population.

Model	AICc	Delta AICc	AICc Weights	Model Likelihood	Num. Par	Deviance
$\Phi(\bullet)_{(\text{Cort})} (\text{Cort-sq}) =$ $p(\bullet)$	166.55	0	0.44	1	3	160.26
$\Phi(\bullet) = p(\bullet)$	168.19	1.84	0.17	0.44	1	166.15
$\Phi(\bullet)_{(\text{Cort})} = p(\bullet)$	168.53	1.98	0.16	0.37	2	164.39
$\Phi(t) \neq p(\bullet)$	172.13	5.57	0.03	0.06	8	154.28
$\Phi(t) = p(t)$	175.67	9.12	0.00	0.01	7	160.26
$\Phi(t) \neq p(t)$	182.89	16.35	0.00	0.00	13	151.91

Notes: Mean  $\hat{c} = 1.00$ . Time dependence is indicated with (t); constant over time is indicated with ( $\bullet$ ). In some models, corticosterone  $_{(\text{Cort})}$  alone or combined with its square (Cort-sq) were linear or curvilinear covariates respectively; those without these subscripts had no effect of corticosterone.

## Figures

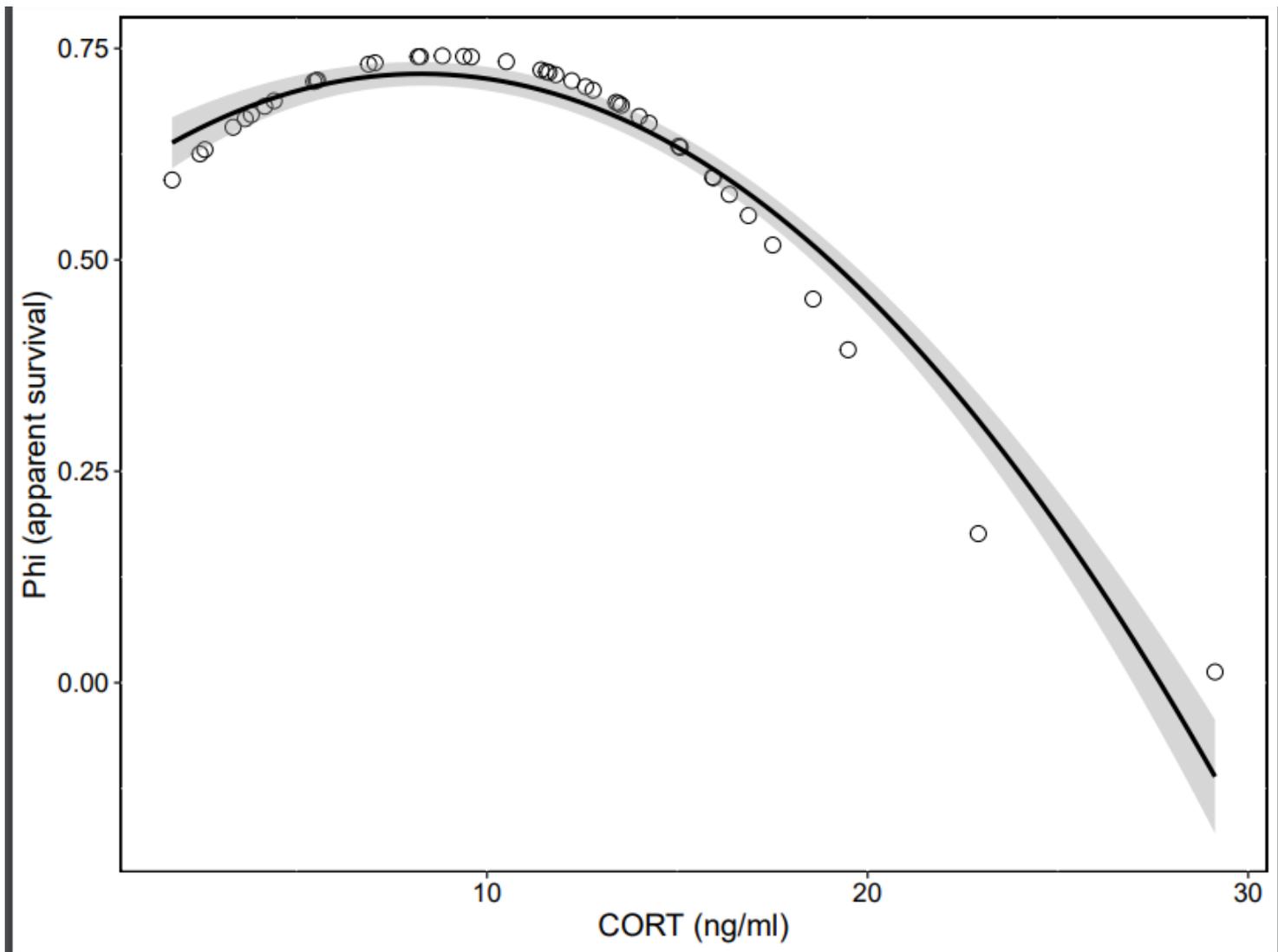
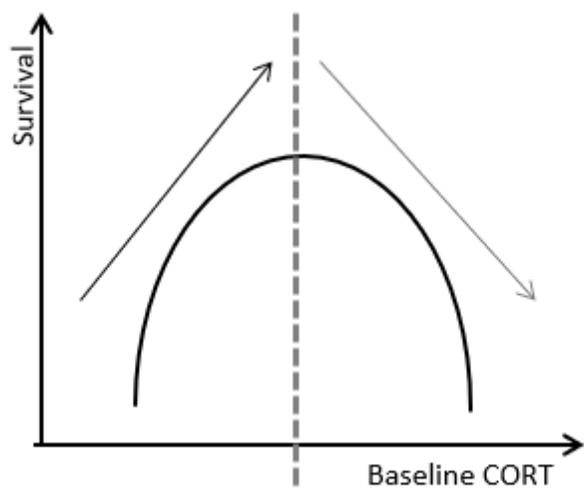


Figure 1

Relationship between baseline Cort levels and inter-annual apparent survival in the Thorn-tailed Rayadito in the high latitude population.



## Figure 2

The “cort-optimal hypothesis”: the dotted line represents the optimal between baseline Cort and survival.  
Black arrow: “cort-activity hypothesis”; Grey arrow: “cort-fitness hypothesis”.