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Article *in* Proceedings of the Royal Society B: Biological Sciences · January 2017

DOI: 10.1098/rspb.2016.2538

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Cite this article: Lin J-W, Chen Y-R, Wang Y-H, Hung K-C, Lin S-M. 2017 Tail regeneration after autotomy revives survival: a case from a long-term monitored lizard population under avian predation. *Proc. R. Soc. B* **284**: 20162538. http://dx.doi.org/10.1098/rspb.2016.2538

Received: 16 November 2016
Accepted: 14 December 2016

Subject Category:
Ecology

Subject Areas:
behaviour, ecology, evolution

Keywords:
costs of reproduction, defence behaviour, fidelity costs of regeneration, male-biased mortality, predation efficiency, sexual dichromatism

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Electronic supplementary material is available online at https://dx.doi.org/10.6084/m9.figshare.c.3653189.

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Tail regeneration after autotomy revives survival: a case from a long-term monitored lizard population under avian predation

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Caudal autotomy in lizards has intrigued scientists for more than 100 years. Because of the relative lack of literature under natural conditions, the complicated association among field autotomy rate, real predation pressure, the long-term cost of tail loss, and the benefit of regeneration remains equivocal. In this study, we conducted a 7-year capture–mark–recapture (CMR) programme with a wild population of a sexually dichromatic lizard, *Takydromus viridipunctatus*. We used autotomy indexes and a contemporary bird census mega-dataset of four predatory birds as predictors to examine the association between tail loss and predation pressure. We further estimated the survival cost of tail loss and alleviation by regeneration under natural conditions through CMR modelling. We found that large and small avian predators affect lizard survival through the following two routes: the larger-sized cattle egret causes direct mortality while the smaller shrikes and kestrels are the major causes of autotomy. Following autotomy, the survival rate of tailless individuals over the next month was significantly lower than that of tailed individuals, especially males during the breeding season, which showed a decline of greater than 30%. This sex-related difference further demonstrated the importance of reproductive costs for males in this sexually dichromatic species. However, the risk of mortality returned to baseline after the tails were fully grown. This study indicates the benefit of tail regeneration under natural conditions, which increases our understanding of the cost–benefit dynamics of caudal autotomy and further explains the maintenance of this trait as an evolutionarily beneficial adaption to long-term predator–prey interactions.

1. Introduction

Autotomy, the voluntary shedding of an appendage to evade entrapment [1], is perhaps the most dramatic and energetically costly anti-predator behaviour in animals. It has been observed in diverse animal taxa including both invertebrates and vertebrates that detach a variety of body parts [2–8]. In addition to the well-known immediate survival benefit of this tactic, the costs to the individual after detachment have also received much attention in recent decades, which has increased our understanding of the cost–benefit dynamics of autotomy and its evolutionary trajectory [2,7,8].

Caudal autotomy in lizards is perhaps the most famous case of a body-shedding tactic, and it has intrigued scientists for over 100 years [3,9,10]. Species from at least two-thirds of lizard families have the capability to lose and regenerate their tails [11–13]. During this process, contracting muscles split the weak structure of the tail vertebra, which causes the tail to separate from the body and enables the lizard to flee from the grip of a predator [6]. The post-autotomy tail acts as a distraction that writhes and wiggles to draw the attention of the predator away from the owner of the tail [6,14,15]. Many previous studies have shown that tail autotomy could increase the immediate survival rate when lizards encounter predators [16–18], and subsequent studies also suggested that the risk of predation might enhance the evolution of autotomy [19–21].

Despite the long-term interest in tail loss in lizards, some issues remain the subject of debate. First, the degree of association between the frequency of caudal autotomy and predation pressure under natural conditions is controversial. In recent decades, researchers have debated the ecological relevance of autotomy rate in the wild as follows: does it reflect the real predation pressure? Or does it reflect predation 'inefficiency' ([22–24], reviewed in [13])? The inconsistent results concerning the relationship between the field autotomy rate and predation pressure [20,21] reveal that the debate is ongoing. As the field autotomy rate of lizards is influenced by the temporal and seasonal fluctuations of the abundances of multiple predators, the association between field autotomy rate and predation pressure would be obscured if researchers only focus on a short timescale. Surprisingly, long-term studies of autotomy in lizards are extremely rare.

Second, although the costs of tail loss and regeneration have been well studied in captivity, the long-term consequences have been less well explored in the wild [3,8]. Many studies have documented the intrinsic impacts of tail loss, including energetic impairment [25–27], decreased agility and/or activity ([28–30] reviewed in [31]), and the loss of the opportunity to shed the tail in a subsequent predatory encounter [12]. All of these factors are assumed to contribute to the ultimate cost—a decline in mating success [32–34] and survival [12,26,35]. Nevertheless, most studies that were performed in the laboratory or within artificial or semi-natural environments only showed an effect for a short time following tail loss. Only a handful of studies have focused on the long-term consequences of autotomy in the wild, particularly as they relate to survival. The rarity of field studies and their inconsistent results have perpetuated the ambiguity of the long-term costs of tail loss. For example, the contradictory results from studies of *Uta stansburiana* (positive evidence in [26,35] but not in [25,36]) indicate that understanding the long-term effect of autotomy on survival remains elusive.

Similar to autotomy, the long-term consequences of regeneration have also rarely been addressed. Regeneration is an energetically expensive process that could exert serious costs on an individual, but this trait is widely maintained in a variety of squamata taxa, which hints at the potential benefit of this strategy. The adaptive hypothesis of regeneration [7] predicts that the regrowth of a shed structure could alleviate the survival cost of autotomy, but little is known about this benefit following regeneration under natural conditions.

Field demographic studies over a long timescale provide a straightforward solution to these debates. In this study, we conducted a 7-year capture–mark–recapture (CMR) experiment on a wild population of the sexually dichromatic green-spotted grass lizard, *Takydromus viridipunctatus*. Members of the genus *Takydromus* are 'grass swimmers' with an elongated body shape and an extremely long tail (2.5–4.2 times the snout–vent length (SVL), depending on the species [37,38]). These lizards inhabit open grasslands and exhibit a unique sleeping behaviour in which they perch almost exclusively on the long, soft, thin leaves of *Miscanthus* or other Gramineae grasses. This behaviour is believed to prevent predation by rodents, shrews, and serpents from the ground at night. These lizards are usually non-territorial, forming extremely high population densities in suitable microhabitats with no pronounced male–male competition [39–41], limiting the potential for intraspecific interactions to result in tail loss. Finally, sympatric owls (*Otus* spp.) have never been observed to prey on this lizard. All these observations support the conclusion that diurnal birds are likely the major predators contributing to green-spotted grass lizard mortality and tail loss (electronic supplementary material, figure S1).

In this study, we incorporated data on lizard survival and caudal autotomy with the data on contemporary dynamics of four major bird predators from a national bird watching mega-dataset. Our objectives were to (i) inspect predator abundance versus lizard tail loss and survival rates to determine the relationship between field autotomy and predation efficiency, (ii) estimate the survival rates of tailed and tailless individuals to understand the long-term consequences of autotomy on survival, and (iii) examine the alleviation of the survival cost of autotomy through tail regeneration to determine the benefit of this evolutionary tactic. With more than 20 000 captures of more than 11 000 individual lizards over the past several years, this is one of the first long-term studies of the cost–benefit relationship of tail autotomy and regeneration in the wild.

2. Material and methods

(a) Lizard study system

The green-spotted grass lizard, *T. viridipunctatus* (Squamata: Lacertidae), is a small lacertid (SVL of approx. 48 mm in adults; [42]) with prominent sex dichromatism. The breeding season lasts from early May to late September, when seasonal courtship colouration occurs in males (intense green spots on their lateral sides), and V-shaped bite marks from copulation can be observed on females. The long-term monitoring of a closed population of *T. viridipunctatus* began in 2006 at Jinshan Cape of northern Taiwan, a coastal promontory surrounded by ocean and developed regions; thus, the dispersal probability is relatively low. The vegetation on the cape is primarily grassland (the dominant species are *Miscanthus sinensis*, *Bidens pilosa*, and *Wedelia triloba*) with a mosaic of patches of secondary forest. There are relatively few terrestrial predators; no carnivores have ever been recorded, and serpent abundance is very low.

Since May 2006, monthly CMR lizard surveys have been conducted one night per month, and the data used in this study cover 7 years from February 2007 to August 2013. Seven to 12 experienced fieldworkers searched several transects totalling 800 m in length and captured all of the observed individuals by hand as they slept on *Miscanthus* leaves. Captured lizards were weighed to the nearest 0.01 g using an electronic scale, and their SVLs were measured to the nearest 0.01 mm using a digital calliper. For all individuals, we recorded their sex, age class, and tail autotomy index (see below) before uniquely tagging them by toe clipping, which is thought to be the most efficient and least stressful method for marking this kind of small lizard [43]. Our previous study suggested that there was no systematic bias in the capture procedure [41].

Owing to the high population density at the sampling site, the mean number of captured individuals during each sampling event was approximately 233 but exceeded 500 on some occasions. During the 7-year census period, there were 20 552 captures of 11 415 individuals; the recapture rate in the census region ranges from 0.4 to 0.6 during the breeding season.

(b) Evaluation of tail autotomy

We defined three categories of autotomy based on the length, colour, and neural response of the tails. Individuals were recorded as 'tailless' if they had experienced a recent tail loss, which could be distinguished by a wounded, scabbed, or newly regenerating tail. Individuals were classified as 'regenerated' if they had a shorter and differently coloured tail with a weak or absent neural response to tail palpation, while 'intact' tails had not been previously shed. In the following analyses, the autotomy index was applied as a response variable in the multiple regression analysis of the relationship between autotomy and predation pressure and as one of the predictor variables in the survival estimation.

(c) Evaluation of predator abundance

A long-term mega-dataset of all the bird species in Taiwan has been collected by the Chinese Wild Bird Federation from bird watchers and researchers throughout the country. In our study site, the following four species of birds are the major predators of *T. viridipunctatus*: the black drongo (*Dicrurus macrocercus*, resident), the cattle egret (*Bubulcus ibis*, summer migrant), the common kestrel (*Falco tinnunculus*, winter migrant), and the brown shrike (*Lanius cristatus*, absent only in summer); thus, we selected all records in the database of these four species from Northern Taiwan from 2007 to 2013. Considering that autotomy is the consequence of recent predation, we summed the records of each of the four birds from 30 days prior to a capture event to estimate recent (past) predator abundance to examine the association between predation and autotomy rates. On the other hand, we summed the records of the four birds until the next capture occasion to estimate the subsequent (future) predator abundance for survival analysis.

We used principal component (PC) analysis to reduce the four bird predators into two principal components as indexes of predation pressure and then used these indexes as predictor variables to test their effects on caudal autotomy and survival rates. The first two principal components of both recent and subsequent predation pressures explained 85% of the total variance, and both of their eigenvalues were greater than 1 (electronic supplementary material, table S1). The abundances of shrikes and kestrels were prominent in PC1, while the major loading in PC2 was the abundance of cattle egrets; the black drongo contributed evenly to both PCs (electronic supplementary material, table S1).

(d) Correlation between caudal autotomy and predation pressure

We examined the association between predation pressure and caudal autotomy in *T. viridipunctatus* using logistic regression analysis. Considering the sexual dichromatism and breeding season of the lizard, we incorporated sex, season, and the two principal components of recent predation pressure as predictor variables, using recent autotomy (tailless versus intact) as a nominal response variable to build the regression models. We first used forward selection procedures (both the enter and leave probabilities were equal to 0.10) to choose useful predictors from the four predictor variables. We then examined the significance of the model with the chosen variables and their interactions, and inspected the relationship between autotomy rate and the predictors. The data from juvenile and recaptured individuals were excluded from this analysis to prevent potentially confounding effects of size and repeat sampling. Statistics were performed in JMP®, v. 7 (SAS Institute Inc.).

(e) Survival analysis

We implemented the Cormack–Jolly–Seber (CJS) model in Program MARK [44] to estimate the survival rate and test the effects of the predictors. The CJS model simultaneously estimates the survival (φ) and recapture probability (p) between capture occasions, which allows users to incorporate categorical and/or continuous variables as predictors to explain both probabilities. In this study, the monthly survival rate was treated as a linear function of the caudal autotomy index and the two principal components of the subsequent predator abundance while considering the effects of sex and season (breeding and non-breeding)

The time-varied capture probability was first supported by comparing all possible models, and we then tested the significance of the effects of the categorical predictors and continuous predictors on survival with time-varied capture probability in two different stages (see the electronic supplementary material for details). First, we built 19 models with different sets of categorical predictors, including autotomy index, season (breeding and non-breeding), and sex (electronic supplementary material, table S2), to know the effects of the categorical predictors. Second, based on Akaike's information criterion, we used two of the best-supported models ($\varphi_{\mathrm{sex}+a+s+\mathrm{sex}\times a+a\times s}\ p_t$ and $\varphi_{a+s+a\times s}\ p_t$) to construct 38 models comprising continuous predictors, the two principal components of subsequent predator abundance (electronic supplementary material, table S3), and then tested the effects of predation. We tested the significance of the predictors in the well-supported models with a likelihood ratio test. Considering the potential influence of total predation and body size on survival, we also examined their effect on survival (see the electronic supplementary material for details).

3. Results

(a) Tail autotomy and predator abundance

A total of 9 396 data points comprising only adults (5 380 individuals) captured from February 2007 to August 2013 were selected from a total of 20 552 data points from the 7-year census (electronic supplementary material, figure S2*a*). The autotomy rate significantly differed between sexes and among different months (figure 1*a*; $F_{12,145} = 11.54$, $p < 0.0001$; no sex × month interaction), and was significantly higher in females than males ($F_{1,145} = 15.73$, $p = 0.0001$; mean: 0.2465 ± 0.0094 versus 0.1935 ± 0.0094). In both sexes, the autotomy rates were lower in summer (July–August) than in winter and spring ($F_{11,145} = 11.15$, $p < 0.0001$).

The abundance of the four avian predators also fluctuated annually (figure 1*b–e*; electronic supplementary material, figure S2*b–e*). The two winter visitors, the brown shrike and the common kestrel, showed a similar decreasing trend in late spring and were totally absent in summer. The black drongo, a common resident in Taiwan, was recorded throughout the year with little fluctuation. As a summer breeder and transient visitor, the cattle egret showed high abundance in the breeding season and low abundance in the non-breeding season with some extreme peaks in the migration months.

(b) Correlation between autotomy rate and predator abundance

The association between autotomy rate and predation pressure was seasonally dependent and sex-specific (figure 2). Sex,

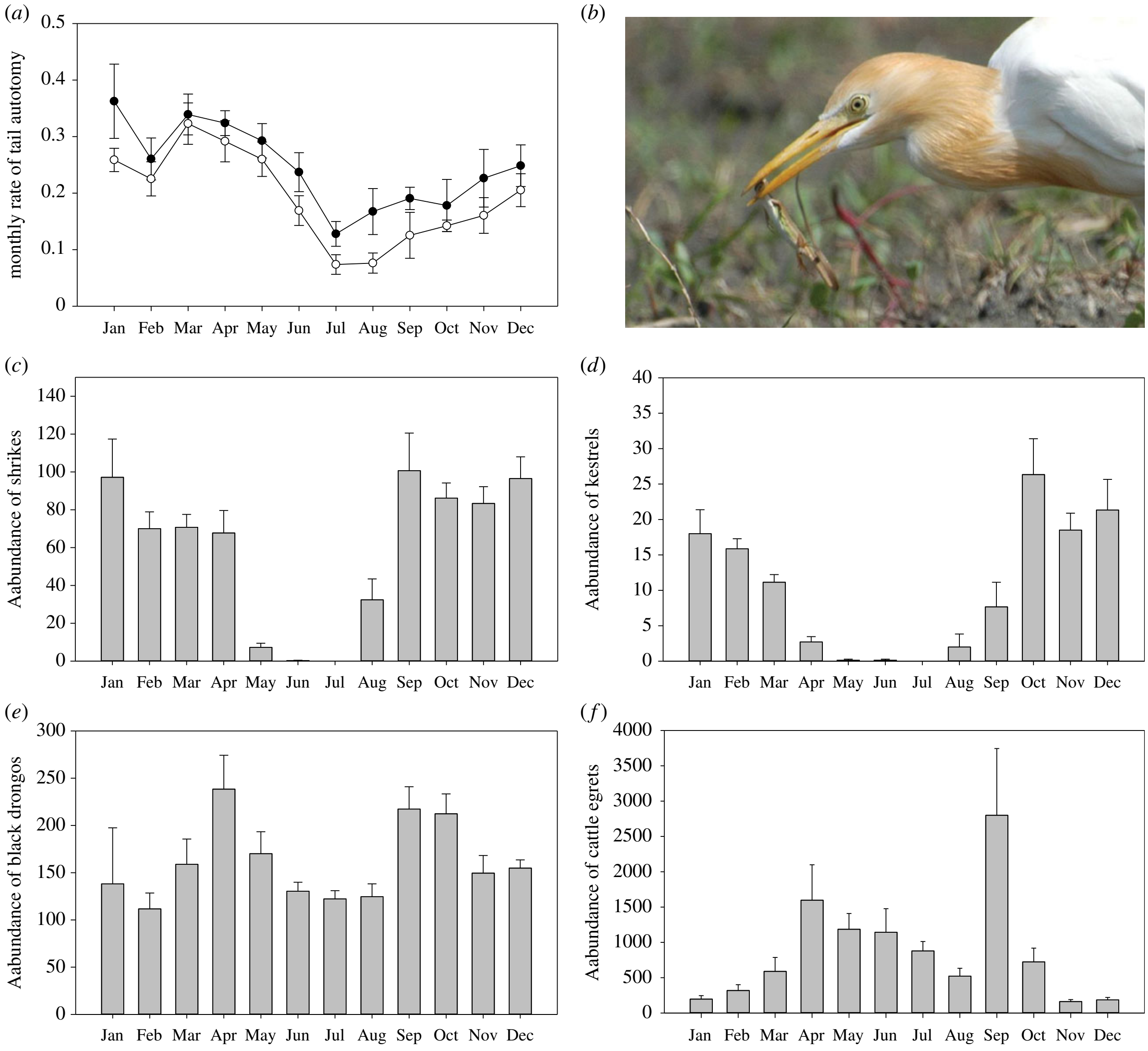

Figure 1. Annual pattern of (*a*) monthly rates of caudal autotomy (mean ± standard error (s.e.)) of adult *Takydromus viridipunctatus* (open circles represent males; closed circles represent females) compared with the abundance of four major avian predators: (c) brown shrike (*Lanius cristatus*), (*d*) common kestrel (*Falco tinnunculus*), (*e*) black drongo (*Dicrurus macrocercus*), and (*f*) cattle egret (*Bubulcus ibis*) from 2007 to 2013. Among the four predators, cattle egret was proved to cause direct mortality on *Takydromus* lizards (*b*, photographed by Dr Chia-Yang Tsai, under the support of Chi Sing Eco-conservation Foundation).

season, and the first component of recent predation pressure (PC1, representing the abundance of shrikes and kestrels) were significant in the forward selection procedure (electronic supplementary material, table S4). However, the second component of recent predation pressure (PC2, representing the abundance of cattle egrets) did not correlate with autotomy rate (Wald/score: $\chi^2 = 0.00004$, d.f. $= 1$, $p = 0.9948$; electronic supplementary material, table S4). The three-way interaction of the chosen predictors was significant (total model: $\chi^2 = 139.22$, d.f. $= 7$, $p < 0.0001$; PC1 × sex × season: $\chi^2 = 4.27$, $p = 0.0389$, table 1), suggesting that all the predictors were associated with caudal autotomy in *T. viridipunctatus* in a complicated way. In the breeding season, both the male and female autotomy rates were positively correlated with the recent abundance of brown shrikes and kestrels (PC1), and this association was stronger in males than in females (table 1 and figure 2) as illustrated by the steeper slope of the male curve. By contrast, during the non-breeding season, the relationship between PC1 and the autotomy rate was negative (figure 2). In the breeding season, the negative association was sex-specific as it was stronger for males compared with females (table 1 and figure 2).

(c) Correlation between survival and predator abundance

Survival rate was negatively associated with both of the subsequent predation pressure PCs. These associations were seasonal and autotomy dependent (figure 3). The best-supported model, $\varphi_{a+s+a\times s+p12+s\times p12}$, involved the autotomy index, season, both subsequent predation PCs, and the interaction terms (electronic supplementary material, table S3). Both predator abundance PCs showed seasonal associations with the survival of *T. viridipunctatus*. PC1 (shrikes and kestrels) negatively associated with the monthly survival rate in the non-breeding season, while the association became weaker in the breeding season. By contrast, PC2 (cattle egrets) negatively correlated with survival rate in the breeding season but had no effect during the non-breeding season (table 2*b* and figure 3). The association between survival and

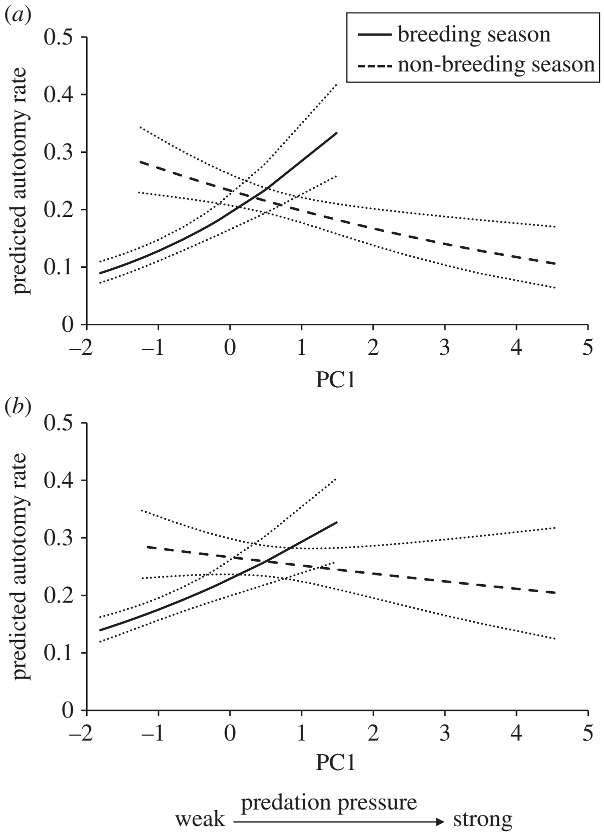

Figure 2. Autotomy rate of (*a*) male and (*b*) female *Takydromus viridipunctatus* against the first component (PC1) which was majorly contributed to by the abundance of shrikes and kestrels. The solid and broken lines denote the predicted autotomy rates in the breeding and non-breeding seasons, respectively. The dotted lines represent the 95% confidence intervals.

shrikes/kestrels was expected because these birds also contribute to the field autotomy rate. However, cattle egrets only associated with survival but not autotomy rate, suggesting that being attacked by an egret might cause direct mortality in lizards without the chance to escape by tail loss. Owing to the even occurrence among different seasons, the contribution of the black drongo was masked by that of the former three predators and did not show a clear pattern in our analyses. There was no significant difference among the slopes of the autotomy categories, suggesting that tailless individuals were not more vulnerable to predators.

(d) Survival cost of tail loss

The survival cost of tail loss was significant in our survival analysis (figure 4). The best-supported model, $\varphi_{\mathrm{sex}+a+s+\mathrm{sex}\times a+a\times s}\ p_t$ (electronic supplementary material, table S2), indicated that survival was associated with autotomy index, sex, and season. Moreover, the effects of autotomy on survival differed between sexes and between breeding and non-breeding seasons (table 2*a* and figure 4). In the non-breeding season, the monthly survival rate of tailless females was approximately 8.74% lower than that of tailed females, while males faced a 17.38% decline in survival (intact females: 0.8636 ± 0.0086, tailless females: 0.7762 ± 0.0256; intact males: 0.8759 ± 0.0074, tailless males: 0.7021 ± 0.0296; figure 4*a*,*b*). In the breeding season, the survival declines in tailless individuals were even more intense in both sexes: a 22.56% decline in females and a 33.93% decline in males (intact females: 0.7922 ± 0.0106, tailless females: 0.5666 ± 0.0302; intact males: 0.8096 ± 0.0100, tailless males: 0.4703 ± 0.0389; figure 4*a*,*b*). This result indicated a crucial survival cost of autotomy, particularly in males during the breeding season.

(e) Benefit of tail regeneration

We found an enormous survival benefit of tail regeneration in both sexes that was also seasonally dependent (table 2*a* and figure 4). In the non-breeding season, there was a 7.53% survival rise between females with regenerated tails and those without tails (tailless females: 0.7762 ± 0.0256; regenerated females: 0.8514 ± 0.0090) and a 14.72% rise in males (tailless males: 0.7021 ± 0.0296; regenerated males: 0.8493 ± 0.0088). In the breeding season, the survival differences between regenerated individuals and tailless individuals in both sexes were even greater: 25.40% in females and 34.78% in males (tailless females: 0.5666 ± 0.0302, regenerated females: 0.8206 ± 0.0109; tailless males: 0.4703 ± 0.0389, regenerated males: 0.8181 ± 0.0111; figure 4*a*,*b*). The large difference in survival between tailless and regenerated individuals suggested an enormous alleviation of the survival cost of tail loss following regeneration. Furthermore, there was no significant difference in survival between individuals with regenerated tails and those with intact tails in both sexes and seasons (figure 4*a*,*b*).

4. Discussion

(a) The benefit of tail regeneration

In addition to the severe costs of tail loss, the most novel discovery in this study is the prominent benefit of tail regeneration to survival. The survival rate of regenerated individuals was significantly higher than that of tailless individuals (figure 4), supporting the prediction of the 'adaptive hypothesis of regeneration' [7,8] that reproducing a lost tail confers adaptive benefits. This is the first documentation of the benefit of tail regeneration under natural conditions, which explains the maintenance of this trait as an evolutionary beneficial adaptation to long-term predator–prey interactions. Furthermore, the survival probabilities of individuals with regenerated tails were not significantly different from those of individuals with intact tails. This suggests that the fidelity cost of regeneration [7,8] is relatively small and a regenerated tail works as well as an intact one, despite the incomplete neural function of the regrown appendage.

Tails play a functional role in lizard locomotion [29,31,45], particularly in species with long tails [29] such as *Takydromus* (2.5–4.2 times the SVL, depending on species). A previous study of *T. septentrionalis* showed an enormous impairment of locomotor performance following the removal of a large proportion of the tail, which supported its function in the agility [46] of this 'grass swimmer'. In *Takydromus*, regenerated tails are usually as long as the originals and retain most of the original functions, such as physical supports when moving through dense grass. Tail function and the significance of tail length in such grass swimmers are worthy of investigation considering the biomechanical context of grassland habitats.

In addition to locomotion functions, regenerated tails also recover the function of distracting predators during attacks. Regenerated tails of *Takydromus* may again be lost anterior to the initial break, and this was observed in some

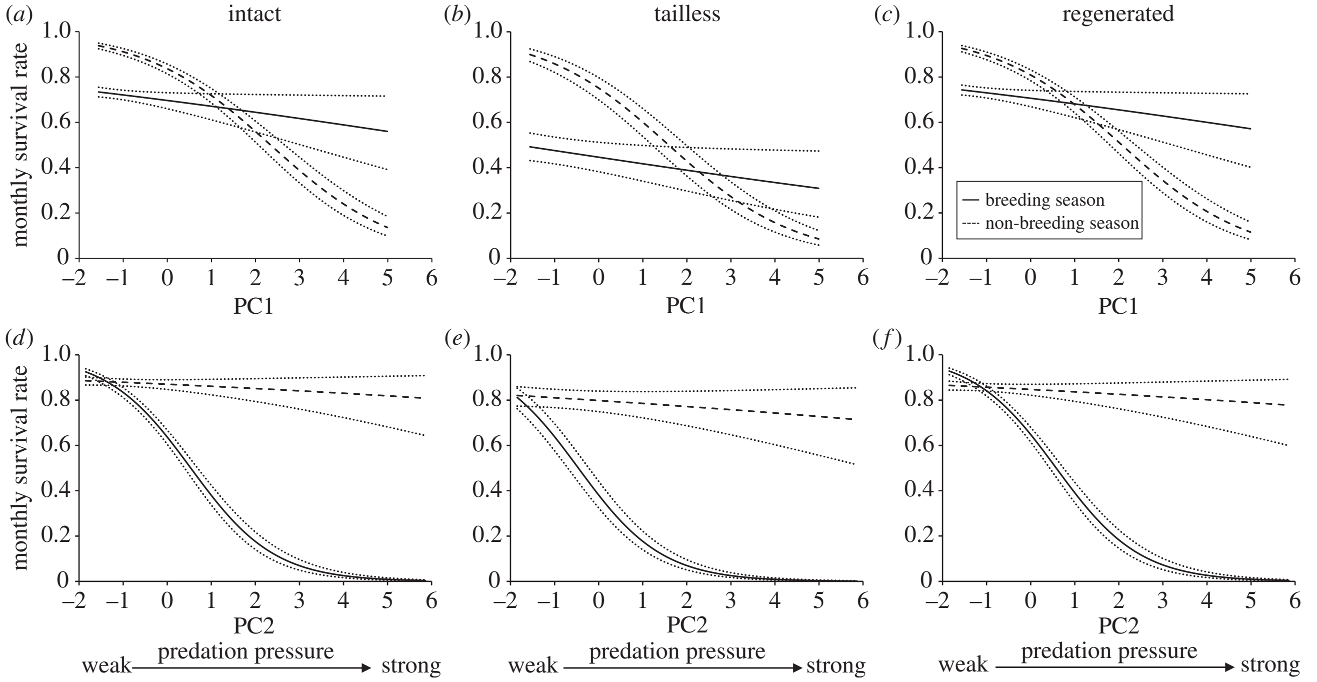

Figure 3. Monthly survival rates of intact (*a*,*d*), tailless (*b*,*e*), and regenerated (*c*,*f*) individuals against PC1 (majorly contributed to by the abundance of shrikes and kestrels) and PC2 (majorly contributed to by the abundance of cattle egrets) of subsequent predator abundance. The solid and broken lines denote the estimated survival rates in the breeding and non-breeding seasons, respectively. The dotted lines represent the 95% confidence intervals.

Table 1. The logistic regression model of monthly caudal autotomy in *Takydromus viridipunctatus*.

effect	coefficient	s.e.	d.f.	χ^2	p
constant	−1.9111	0.0767			
PC1	−0.2075	0.0690	1	9.3064	0.0023
sex (female)	0.1775	0.1115	1	2.5275	0.1119
season (breeding)	−0.2355	0.1244	1	3.6152	0.0573
PC1 × sex	0.1316	0.1008	1	1.7042	0.1917
PC1 × season	0.7002	0.1016	1	46.9361	<0.0001
sex × season	0.0320	0.1731	1	0.0342	0.8532
PC1 × sex × season	−0.2920	0.1413	1	4.2659	0.0389

individuals who were repetitively recaptured during the long-term census. This defence mechanism, although useless when encountering a cattle egret, helps lizards escape attacks from shrikes and kestrels. This observation may explain the increase in survival rate after tails were fully regrown.

(b) The cost of tail loss

We found a great survival cost following tail loss in the wild by means of a long-term population census. Although a long-term cost of caudal autotomy has been assumed for decades, only a handful of studies have been performed under natural conditions, and more than half found no evidence of impaired survival [25,26,35,36,47]. In addition, this cost is sex-specific and seasonally dependent with males experiencing a more serious cost than females, which highlights the significance of the intrinsic differences between the two sexes and the impact of the reproductive cycle on the cost of tail loss.

Comparing the slopes of survival–predation relationships clarified the source of the higher mortality following tail loss. The slopes among the intact, tailless, and regenerated lizards were not significantly different, which suggested that the negative effect of predation was no greater in tailless individuals than in tailed individuals. It implied that the survival cost of tail loss mainly stemmed from the physiological allocation of resources within individuals rather than a second encounter with predators. In the case of *Eutropis multifasciata*, researchers showed a significant decrease in immunocompetence after tail loss which would increase the probability of disease or infection. Therefore, autotomy may associate with some critical physiological functions that are linked to survival [27].

Furthermore, male and female lizards showed differing survival costs of autotomy in this study. This phenomenon is especially prominent in the breeding season; male survival decreases by 33.93% after tail loss compared with 22.56% in females. Previous studies have found associations among sexual dimorphism, ornamentation, parasitism, and male-biased mortality [48–51], and immune function might again play a crucial role in the relationships among these life-history factors [52,53]. Our recent studies confirmed a testosterone-mediated trade-off between the nuptial green colouration and immunocompetence in the green-spotted grass lizard, which

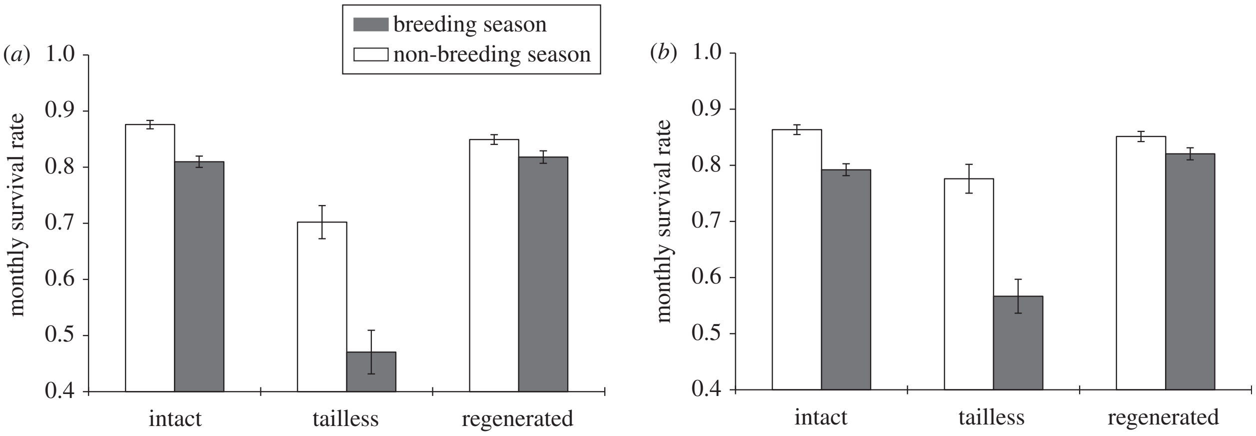

Figure 4. Monthly survival rates of (*a*) male and (*b*) female intact, tailless, and regenerated individuals. The closed bars are the estimated survival rates in the breeding season, while the open bars represent those in the non-breeding season.

Table 2. The logit link function parameters of the two best models of the monthly survival rate of *Takydromus viridipunctatus* for categorical and continuous predictors.

			95% CI	
parameter	**coefficient**	**s.e.**	**lower**	**upper**
(*a*) best model from model selection for categorical predictors: $\varphi_{\text{sex}+a+s+\text{sex}\times a+a\times s}\ p_t$				
intercept	0.8571	0.1417	0.5794	1.1348
autotomy 1[a]	1.0972	0.1532	0.7971	1.3975
autotomy 2[a]	0.8718	0.1539	0.5701	1.1734
sex (female)	0.3868	0.1442	0.1041	0.6695
season (breeding)	−0.9760	0.1998	−1.3676	−0.5843
autotomy 1 × sex	−0.4955	0.1539	−0.7971	−0.1939
autotomy 2 × sex	−0.3697	0.1546	−0.6728	−0.0666
autotomy 1 × season	0.4687	0.2205	0.0367	0.9008
autotomy 2 × season	0.7506	0.2250	0.3095	1.1916
(*b*) best model from model selection for predation: $\varphi_{a+s+a\times s+p12+s\times p12}$				
intercept	1.0814	0.1394	0.8082	1.3546
PC1	−0.6963	0.0375	−0.7698	−0.6228
PC2	−0.0784	0.0621	−0.2001	0.0433
autotomy 1[a]	0.5263	0.1383	0.2552	0.7974
autotomy 2[a]	0.3377	0.1398	0.0636	0.6118
season (breeding)	−1.6155	0.2208	−2.0482	−1.1828
PC1 × season	0.5783	0.0723	0.4366	0.7200
PC2 × season	−0.9738	0.0919	−1.1540	−0.7938
autotomy 1 × season	0.5204	0.2167	0.0958	0.9451
autotomy 2 × season	0.7558	0.2190	0.3265	1.1851

[a] autotomy 1 = intact; autotomy 2 = regenerated.

were further linked to parasitism and survival in this species [41,54]. The severe survival cost of autotomy in the breeding season, especially in males, might result from complicated interactions among tail loss, immunity, pathogens, and reproduction.

(c) Avian predators influence lizard survival via two routes

Our results showed that the brown shrike and the common kestrel reduced both autotomy and survival rate, while the cattle egret only influenced survival rate. This suggested that avian predators control the population of *T. viridipunctatus* by means of two routes: the small predators, shrikes (17–20 cm, 27–37 g) and kestrels (33–39 cm, 136–314 g), promote caudal autotomy and subsequent survival costs, while the large predator, the cattle egret (50 cm, greater than 400 g), reduces survival directly. The black drongo contributes evenly to both effects year round but at a slightly lower magnitude than the other three predators.

The ecological significance of the autotomy rate in the wild has been extensively debated for several decades, due to contrary inferences about autotomy rate and predation ([22,55], review in [13]), and mathematical ecologists have suggested that the autotomy rate, survival rate, and predation pressure should be measured in the field to address this controversy [55]. By incorporating all these factors under natural conditions, our results strongly suggest that only evaluating the autotomy rate is insufficient to assess predation pressure. The *Takydromus* study system establishes a framework for the long-term study of autotomy and predation and provides a satisfactory answer to this long-lasting debate.

5. Conclusion

Our study found clear evidence to answer long-standing questions about caudal autotomy. Large predators (i.e. cattle egrets) cause direct mortality, while small predators (i.e. shrikes and kestrels) promote both autotomy and mortality. There was a severe survival cost of tail loss in *T. viridipunctatus*, particularly in males during the breeding season, which led to a greater than 30% decrease in survival. The sex-related difference in the impact of tail loss further highlighted the importance of reproductive costs in this sexually dichromatic species. Most importantly, the risk of mortality dramatically decreased following tail regeneration, demonstrating the benefit of this energetically costly response and further explaining the maintenance of this trait as an evolutionary beneficial strategy to long-term predator–prey interactions.

Data accessibility. Data are available on Dryad: http://dx.doi.org/10.5061/dryad.2d1f6.

Authors' contributions. Y.-R.C. and S.-M.L. initiated the programme; J.-W.L., Y.-R.C., Y.-H.W., and S.-M.L. conducted the research. K.-C.H. analysed the bird census data, and J.-W.L. analysed the autotomy and survival data. J.-W.L. and S.-M.L. wrote the manuscript.

Competing interests. We declare we have no competing interests.

Funding. This experiment was supported by Ministry of Science and Technology, Taiwan (NSC 96-2628-B-034-001-MY3 and MOST 102-2621-B-003-003-MY3) and was performed in accordance with Wildlife Conservation Act in Taiwan.

Acknowledgements. We want to deliver our special thanks to Chinese Wild Bird Federation for providing their precious bird records without hesitation. We also thank Dr Pei-Jen Shaner for her kind help in data analyses, and Miss Hui-Yun Tseng for her great assistance in using high-speed computer equipment. The 20 000 lizard CMR records were achieved under the great help from all members in S.M.L.'s lab as listed in the electronic supplementary material.

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