Curse of the black spot: spotting negatively correlate with fitness in black grouse *Lyrurus tetrix*

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Running head: Melanin spots and male fitness

Summary

There is growing evidence that achromatic plumage can act as honest indicators of male quality. In some species with areas of white plumage, black melanin spots can be found on parts of the feathers. The functional significance of these spots and the relationship with male quality is yet poorly understood. We investigated the relationship between black melanin spots in an otherwise totally white ornament, the undertail covert, in relation to age, fitness and covariance with past and present expression of sexual traits, in the lekking black grouse *Lyrurus tetrix.* We found that spots at tips of feathers (tip spots) were negatively related to survival and reproductive success, and covaried negatively with current fighting rate. They also covaried positively with past fighting rate, suggesting high investment in fighting leads to carryover effects on male condition. In contrast, spots found further down the feather (vane spots) were unrelated to fitness and morphological and behavioural trait expression. Our results show that melanin spots can indicate some relationship with male quality and that the location of the spots has some importance in this relationship. However, the exact drivers of melanin spot expression and how these link to male quality, are currently unknown.

Keywords: achromatic, melanin, lekking,

INTRODUCTION

Achromatic plumage patterns (black, white and grey) are found widely across bird species (McGraw 2006; Stoddard and Prum 2011). There are two different types of melanin pigments, eumelanin and phaeomelanin, with grey and black colorations resulting from a higher concentration of eumelanin relative to phaeomelanin (Haase et al. 1992; McGraw 2006). Alongside melanin-based plumage, white plumage results from the scattering of light in all directions by unpigmented feather keratin (Prum et al.1999) and requires neither pigment nor specialized feather structure. In the past, most research has focused on the function of brightly colored ornaments, but recent research suggests that achromatic plumage can be an essential component of sexual signalling in some species (Mennill et al. 2003), especially being an important part of visual display (see Galván 2008). Moreover, recent studies have demonstrated that achromatic plumage may also act as a condition-dependent or as condition-related signals (McGlothlin et al. 2007; Gladbach et al. 2011; Roulin 2015) and in some cases relates to components of fitness (Doucet et al. 2005; Guindre-Parker et al. 2012). Most work has focussed on black plumage, because it is assumed that white feathers are cheap to produce (Török et al. 2003). However, white feather patches may also be condition-dependent (Gustafsson et al.1995; Török et al. 2003; Hanssen et al. 2006; Blanco and Fargallo 2013; though see Lehikoinen et al. 2010), and likely to have some production costs (Vágási et al. 2010). Combined, it means that either the production of black or white plumage may be condition-dependent or condition-related depending on the context.

Our understanding of the condition-dependence of achromatic plumage, hinges on the control or lack of control over melanin production. Melanin is synthesized endogenously in the melanocytes that occur primarily in the dermis; the melanocytes migrate into the dermal pulp of the developing feather germ, where the melanin is packaged into melanosomes which are transferred to keratinocytes for deposition into developing feathers (Yu et al. 2004;

Ducrest et al. 2008). Despite our knowledge of the process of melanin production, we do not understand how melanin-based pigmentation is regulated, i.e. whether it is caused by presence/absence of melanocytes, formation or activities of melanosomes, or the transfer of melanosomes to keratinocytes (Yu et al. 2004). Roulin (2015) distinguished two scenarios where melanin-based colouration ways could covary with condition: in the first, condition-related signalling, factors influencing body condition indirectly impact melanin coloration, whereas in condition-dependent signalling, coloration and condition are causally-linked. There are a number of potential opportunities for condition-dependence to influence melanogenesis and the production of depigmented areas (reviewed by Guindre-Parker and Love 2014), because melanin-based coloration have been associated with physiological and behavioural functions (Ducrest et al. 2008) and positively and negatively related to fitness (Roulin et al. 2003; Meunier et al. 2011) in a context-dependent manner (e.g. Roulin et al. 2008a, b).

Most work had focussed on the size and shape of melanin or depigmented areas. In contrast, melanin spotting has received considerable attention but in more limited numbers of species. There have been extensive investigations in barn owls *Tyto alba* (e.g Roulin et al. 1998), and to a lesser extent in other species (salmonids *Salmo salar* & *Oncorhyncus mykiss*: Kittelsen et al. 2009; snow buntings *Plectrophenax nivalis*: Guindre-Parker et al. 2013). Evidence suggests that spotting is linked to components of fitness such as reproduction (Guindre-Parker et al. 2013) and survival (Roulin et al. 2010), suggesting a link between the ability to control melanin production and underlying condition (e.g. Kittelsen et al. 2009). Melanin spotting, may therefore act as a signal of condition.

The black grouse *Lyrurus tetrix* is a lekking galliform that has been studied extensively in the context of sexual selection and sexual traits (see Kervinen et al. 2015, 2016). Traits include tail (lyre) length and quality (Höglund et al. 1994), the size of testosterone-dependent red eye combs (Rintamäki et al. 2000), body mass (Lebigre et al. 2013) and blue structural coloration (blue chroma) of breast feathers (Siitari et al. 2007). Females also prefer mating with males that have high lek attendance (Alatalo et al. 1992), fight frequently and successfully against other males (Hämäläinen et al. 2012), and occupy central territories on leks (Hovi et al. 1994). The dominant coloration of black grouse is eumelanin-based i.e. black, but there are also depigmented patches on the upper and underside of the wing and the conspicuous white undertail coverts. These undertail coverts are held open in a fan shape during calling on the lek (Figure 1; Höglund et al. 1994). However, black grouse tail fans are not always totally white; melanin spotting of various sizes can be found in different parts of the feathers (Figure 1). Despite being used as individual identifiers on leks (e.g. Alatalo et al. 1992), the functional significance of these spots is unknown to date. To address this issue, we therefore tested the relationship between melanin spotting on a white ornament and (a) its age-dependence, (b) its relationship to two major components of fitness (mating success, survival) and (c) their interrelationship with current and past expression of sexual signals in black grouse.

MATERIALS AND METHODS

Capture and handling

During 2004–2010, we collected longitudinal data describing male mating success and multiple sexual traits in five study sites in Central Finland (peat bogs with high visibility, ca. 62°15’N; 25°00’E). In addition, males were monitored during the mating season until spring 2014 to ensure the use of complete cohorts (no ringed males alive) in the analyses. Each study site is a local main lek with 5–40 territorial males, and as local hunting clubs have refrained from hunting on these areas, the age structure of the study population can reasonably be assumed to be natural.

Measurements of morphological traits were carried out annually in January–March by catching birds from the winter flocks with oat-baited walk-in traps (for methods, see Kervinen *et al.* 2012; Lebigre *et al.* 2012). Each captured individual was aged as yearling or older according to plumage characteristics and individually ringed for future identification with an aluminium tarsus ring with a unique serial number and three colored tarsus rings. All captured birds were measured for body mass, lyre (i.e. tail) length, eye comb size and blue chroma coloration of breast feathers (see Siitari *et al.* 2007; Lebigre *et al.* 2012 for details). When captured, the grouse holds the tail fan closed and concealed making it impossible to fully photograph the tail spread manually. Therefore, each feather of the white tail fan was manually inspected and for each individual, the total number of melanin spots and their location (at tip or within the main part of the vane) was recorded (Figure 1).

Mating success, lekking behaviour and survival

Male mating success and lekking behaviour were recorded on the study sites annually during the mating season (late April – early May, Ludwig *et al.* 2006). During this period, leks were daily monitored *ca.* from 3:00 to 8:00 a.m. from hides near the lek arenas (for methods, see Kervinen et al. 2012; Lebigre et al. 2012). Male behaviour was scan sampled at regular intervals and categorised as rookooing, hissing (the two main vocal displays), fighting or inactive (methods and behaviours are described in detail in Höglund et al. 1997). Lek attendance (proportional to the most commonly present male on the same lek), the relative proportion of each behaviour, and males' territory distances from the lek centre (see Lebigre *et al.* 2012 for descriptions of all behavioural attributes) were calculated for all individually identifiable males from the records for males. Whenever recording male activity, the spatial location of each male on the lek was also recorded. Finally, we documented the observed copulations, which are easy to observe, as males flap their wings conspicuously when mounting females, their location and the individuals involved. Males captured during winter or recorded at leks were classified as alive; due to male philopatry for their initial lekking site (Lebigre et al. 2008), males no longer seen on the study sites were considered dead.

Data Analysis

We considered the location of melanin spots as being important, as they may reflect different moments during feather development. We first tested whether there were age-specific patterns of spot expression by fitting a poisson GLMM with spot number (either vane or tip) as a dependent variable, age (linear) and age^2 (quadratic) fitted as fixed factors, and age and individual ring number were fitted as random slopes and random intercepts effect (1+age|id). We then tested the relationship between spot number and survival and annual mating success using binomial and Poisson GLMMs, respectively. Survival (alive=1, dead=0) was tested with age and spot number as fixed effects. Mating success was tested with age, age^2 and spot number as fixed effects. In both models, age and individual ring number were fitted as random slopes and random intercepts effect (1+age|id).

We then tested the covariance between spot number and morphological (body mass, lyre length, blue chroma coloration) and behavioural traits (lek attendance, fighting rate, distance from lek centre) using Poisson GLMMs; morphological or behavioural traits were fitted as fixed effects in separate multivariate analyzes. Distance from lek centre was included as linear and non-linear functions. This is because distance from lek centre is acquired over a number of years, and high quality but young males may be at the lek periphery and move inwards as they age whereas old males of declining condition may be nearer the lek center but moving outwards (Kokko et al. 1998; Kervinen et al. 2015). Age has a very strong effect on the trait expression, particularly between ages 1 and 2, which is likely to exaggerate any covariance (Kervinen et al. 2015). As a consequence, we tested yearlings and adult birds (≥2 years old) separately and included age as a second random effect in the latter analyzes.

Lastly, we tested for a lag between past trait expression and current spot number. To do this, we analyzed the number of spots (vane or tip) and used the traits (morphological or behavioural) expressed in the previous year. Again, the age-specific increase in trait values between age 1 and 2 is likely to have an important impact on results, so we analyzed 2 year old birds against their yearling (1 year old) values separately from older birds (≥2 years old). All models were run in R version 3.2.1 (R Core Team 2015) with GLMMs using the lme4 package (Bates et al. 2015). In total, we have data for 152 individual males and 325 counts of spots.

RESULTS

Age and spot numbers

There was a significant negative relationship between vane spots and age and a significant positive quadratic relationship (GLMM: linear age, $\beta \pm SE = -0.89 \pm 0.10$, $Z = -9.10$, $P < 0.001$; quadratic age, $\beta \pm SE = 0.12 \pm 0.02$, $Z = 7.29$, $P < 0.001$), which indicated that young and old individuals had more vane spots than prime/middle age males (Figure 2a). This pattern is opposite to that of tip spots which were a significantly positively related to male age with a significant negative quadratic effect (GLMM: linear age, $\beta \pm SE = 1.91 \pm 0.17$, $Z = 10.82$, $P < 0.001$; quadratic age, $\beta \pm SE = -0.18 \pm 0.02$, $Z = -7.44$, $P < 0.001$), which meant that young and old birds had fewer tip spots than prime/middle age males (Figure 2b). There was no correlation between the number of vane and tip spots (r_s=-0.02, P=0.645).

Melanin spotting and fitness

The number of vane spots was unrelated to male survival and annual mating success while accounting for age (Table 1a and c; Figure 2a). In contrast, individuals with larger numbers of tip spots had reduced survival and lower annual mating success (Table 1b and d; Figure 2b; Figure 3).

Melanin spotting and current sexual signals

The number of vane spots and tip spots were unrelated to any other morphological traits in adults (Table 2). There was a significant negative relationship between vane spots and lek attendance in adult birds (Table 2; Figure 4a), and a non-significant quadratic relationship with distance from lek centre suggesting that birds close and further from the lek centre had fewer vane spots (Table 2). Tip spots were negatively related to fighting rate in adults (Table 2; Figure 4b), and there was a non-significant quadratic relationship with distance from lek centre suggesting that birds very close and furthest from the lek centre had fewest tip spots (Table 2; Figure 4c). For yearlings, there was only a weak positive trend for blue chroma to significantly relate to vane (P=0.066) and unrelated to tip spots (P=0.122), but not for any other morphological trait (Table 3). No behavioural traits were associated with vane or tip spot number in yearlings (Table 3).

Melanin spotting and past sexual signals

The number of vane spots were unrelated to both morphological and behavioural trait values from the previous year in >2 year old adults (Table 3). The number of tip spots were also unrelated to past morphological traits (Table 3), but positively related to fighting rate and distance from lek centre from the previous year (Table 3; Figure 5a and b).

For males which were juveniles in the previous year, there were significant relationships between blue chroma in the previous year and vane and tip spots, but not for any other morphological trait (Table 3). Similarly there was no relationship between vane spots and behavioural traits in the previous year, and a positive trend only for lek attendance (P=0.052) to relate to tip spot number (Table 3).

DISCUSSION

Location differences in spotting

The specific location of melanin spots on white undertail covert feathers of black grouse seems absolutely crucial. Males with more spots at the tips of feathers have lower survival and reproductive success, whereas spots located in the inner or outer vane are unrelated to male fitness. At the same time, there was stronger covariance with past and present behavioural traits in tip spots, when compared to vane spots. It has been previously shown in other species, that a single plumage characteristic can signal multiple components of quality or fitness (e.g. Doucet et al. 2003) but in this case we show that the magnitude and direction of the association of a single signal (white feather melanization), has fine scale difference in meaning. Such differences in the location of the black spot most probably results from differences in the timing of the deposition of melanin granules in the feather follicules by the melanocytes during moult. Indeed, the black spots on the white tail feathers of black grouse are located on the closed pennaceous portions of the feather and individual pennaceous barb ridges grow helically around the follicular collar towards the rachis (Prum and Williamson 2001). This means that melanin is being deposited at the very start of the barb's growth in the case of tip spots, and later on for vane spots. In black grouse, the onset of moult occurs directly after the breeding season (Ginn and Melville 1983) and it has been shown that in a closely related species (the blue grouse; *Dendragapus obscurus*), the under tail coverts are moulted at the same time as the rectrices, right at the end of moulting (Zwickel and Bendell 2004). Moulting in birds has an energetic cost and specific nutrient requirements (Bryant 1997). Depletion of certain resources such as of calcium and cysteine may impact melanization (Stewart and Westneat 2013). For example, gluthathione is used as a cysteine reservoir during moult (Murphy and King 1990), and depletion of glutathione can lead to increased melanogenesis (Galván and Alonso-Alvarez 2008). In addition, melanin production is tightly linked to production of corticosterone (Ducrest et al. 2008). Increased amounts of spotting may therefore reflect greater physiological stress during moult. We unfortunately can only speculate as to how and why the melanin spots occur because we lack detailed physiological measurements in our study system, and addressing this issue will be a key future research question.

Age and covariance with other sexual traits

There was a strong age-dependence of melanin spotting suggesting that the factors driving production of these spots are linked to other age-specific processes. Indeed, vane spots were highest in young and older birds, whereas tip spots number increased with age and within-individual changes were highest at older ages. In barn owls, the number of spots in males declined during young age classes, but not at older ages (Dreiss & Roulin 2010). Many species show maximal trait expression during prime-age (e.g. Vanpe et al. 2007), and in grouse other sexual signals are highest during prime-age (Kervinen et al. 2015). This suggests that potential drivers of spot production are linked to age-specific changes in condition, signalling, regulation or behaviour.

Males of many species have multiple signals of quality. These multiple signals can be used for a number of purposes such as backup signals or multiple messages for mate choice (Candolin 2003; Bro-Jørgensen 2010) and often multiple traits covary positively, even if they have different temporal integration with male quality (Badyaev 2004). Yet, contrary to these expectations age-specific patterns of spotting did not strongly covary with other traits This suggests that tail spots are signalling different components of the condition that are unlinked to the development of other sexual ornaments. This result may confirm past results suggesting that multiple cues can provide different information on male quality (Møller & Pomiankowski 1993, Johnstone 1997, Siitari et al. 2007, Kervinen et al. 2016,). Other studies comparing numbers of black spots have found mixed results. Snow buntings showed a significant negative covariance between total spotting and three current plumage traits (S.L. Guidre-Parker pers. comm.), whereas in barn owls, tail length and body mass (Roulin 2006), but not wing feather traits (Roulin et al. 2013) are related to spotting. We also found limited relationships with previous morphological traits. Only in yearling males were there any significant patterns, with lighter yearling males having more tip spots in the following year, again suggesting that tip spots are linked to males' past condition.

Moulting in black grouse typically occurs during June-September (exceptionally May; Ginn and Melville 1983). This means there is a short temporal separation between past behavioural traits and spot production. Unsurprisingly, the relationship between past traits and tip spots is stronger. We found a positive covariance with past fighting rates and tips spots and a negative covariance between current fighting rate and tip spots and current lek attendance and vane spots. Fighting is a costly activity and high investment leads to large losses in body mass (Hämäläinen et al. 2012). As is widespread in ecology (Harrison et al. 2011), it seems that there is a carry-over effect from high investment in lekking (fighting and lek attendance) from one year to the next; high effort in one year leads to increased spotting the following year. Since the relationship between spotting and behavioural traits is negative in the current year, this suggest that there is some decline in condition between years which spotting is correlating with.

In black grouse and many other species, males nearest to the lek centre are the best quality and have the highest mating success (Hovi et al. 1994; Bro-Jørgensen, and Durant 2003; Stein and Uy 2006); hence, males close to the lek centre are of high quality. Males move closer to the lek centre as they reach prime-age and move further from the lek centre post-prime (Kervinen et al. 2015). There was a positive relationship between distance from lek centre and tip spots in the previous year and a trend for a negative quadratic relationship in the current year. This means that those males closest to the lek centre had few tip spots both in the past and the current year. Again, this suggests that spotting is correlating somehow with male condition or quality.

Fitness effect and spotting

There is typically a strong positive relationship between sexually selected traits and male fitness (Andersson 1994). We found that male black grouse with a large number of tip spots had lower annual mating success and were less likely to survive to the next year. This suggests that the melanisation at the tip spots themselves are honestly signalling some negative component of males current and past condition (Galván and Alonso-Alvarez 2009; Hõrak et al. 2010). In black grouse, reproductive effort leads to significant loss of body mass

(Lebigre et al. 2013), particularly in prime-aged males (Kervinen et al. 2012, 2015). This high reproductive effort is likely to generate high levels of oxidative stress and potentially deplete key antioxidants such as gluthathione (Anderson 1988), which in turn can lead to greater melanin expression (Galván and Alonso-Alvarez 2008). Lekking may also be stressful, and high corticosterone levels would further link to melanin production (Ducrest et al. 2008).

Other studies have shown that the expression of a larger melanin ornaments may honestly signal underlying physiological costs, e.g. reduced survival (Moore et al. 2015), possibly because of the costs of melanin production. For the white feathers of black grouse, we suggest the reverse. It appears that the white feathers themselves either have production costs (Vágási et al. 2010) or that the ability to suppress melanin production is condition-dependent. Similar to our results, spotting seemed to be negative for males of other species; male barn owls with larger melanin spots had reduced survival (Roulin et al. 2010) and male snow buntings with more spotting on white feathers had lower fledgling success (Guidre-Parker et al. 2013).

We do not know whether tip spots themselves are sexually-selected. The tail fan and its intactness has been shown to have a role in female choice in black grouse possibly as a secondary cue in less dominant males (Höglund et al. 1994). The location of tip spots makes them more visible during display. As they additionally seem to honestly indicate some underlying male quality/condition, they have the potential to be used by females during mate choice.

Conclusions

Our results demonstrate that spots at the tip of the undertail coverts of male black grouse were negatively correlated to male quality. Males with more tip spots had reduce performance during lekking, lower mating success and lower subsequent survival. Though tip spots clearly indicated some negative relationship with condition, we have no clear idea why. The melanin spotting provides an important system to further advance our understanding of the mechanistic basis for the control of pigment production and achromatic plumage.

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FIGURE LEGENDS

Figure 1: Photographs showing male black grouse holding their fan open during lek display, with examples of both tip and vane spots.

Figure 2: Mean±SE number age specific variation in the number of (a) vane and (b) tip spots. Number of spots for individuals that died (open boxes) or survived to the following year (filled boxes) are shown.

Figure 3: The relationship between annual mating success and number of tip spots across all age classes is shown.

Figure 4: The relationship (a) current fighting rate the number of vane spots and (b) the current fighting rate and(c) distance from lek centre and number of tip spots

Figure 5: The relationship between number of tip spots (a) fighting rate and (b) distance from lek centre in the previous year.

Table 1: GLMM results for male survival and annual mating success in relation to age and the number of either vane or tip spots.

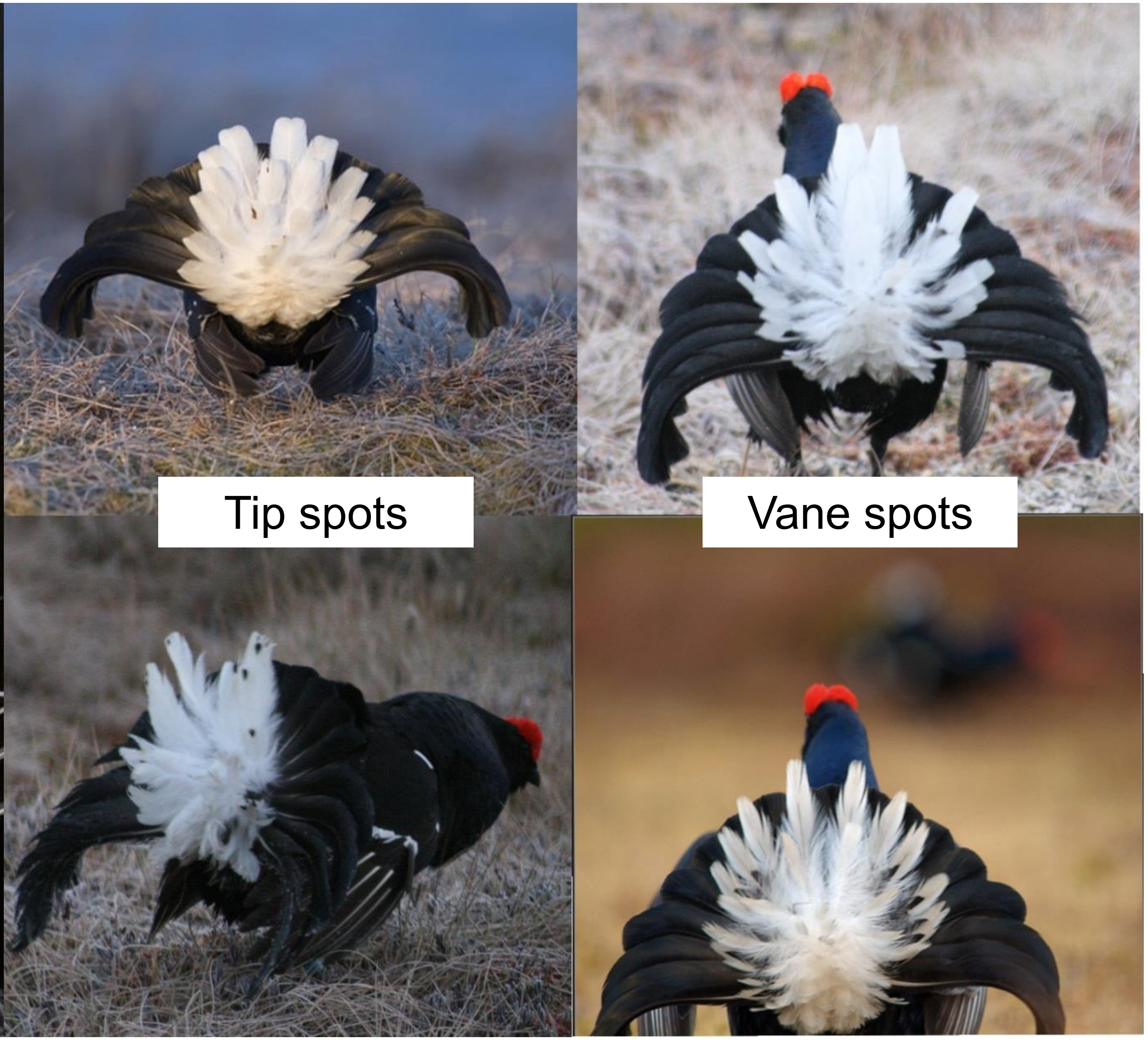
Model	**Parameter**	**β±SE**	**Z**	**P**
(a) Survival	Age	-0.55±0.21	-2.62	0.009
	Vane spots	0.05±0.03	1.51	0.131
(b) Survival	Age	-0.46±0.18	-2.49	0.013
	Tip spots	-0.08±0.04	-2.05	0.041
(c) Annual Mating Success	Age (linear)	4.87±0.62	7.82	<0.001
	Age (quadratic)	-0.66±0.10	-6.86	<0.001
	Vane spots	0.05±0.04	1.28	0.200
(d) Annual Mating Success	Age (linear)	5.17±1.10	8.78	<0.001
	Age (quadratic)	-0.68±0.09	-7.44	<0.001
	Tip spots	-0.07±0.03	-2.07	0.038

Table 2: GLMM outputs for the relationship between vane and tip spots and other sexually selected traits in juvenile and adult black grouse males.

		Juveniles			**Older**		
Model	**Parameter**	**β±SE**	**Z**	**P**	**βs±SE**	**Z**	**P**
Vane spots	Body mass	0.00±0.00	-0.01	0.989	0.00±0.00	0.69	0.491
	Lyre length	0.00±0.00	-0.32	0.752	0.02±0.01	1.68	0.093
	Blue chroma	2.81±1.53	1.84	0.066	3.54±2.64	1.34	0.181
	Red eye combs	0.08±0.05	1.55	0.121	0.08±0.07	1.09	0.277
Vane spots	Lek attendance	0.58±0.54	1.09	0.276	-1.32±0.65	-2.03	0.042
	Fighting rate	-0.06±0.72	-0.08	0.938	0.02±0.04	0.04	0.971
	Distance from lek centre (linear)	0.04±0.02	1.60	0.110	0.04±0.02	1.62	0.105
	Distance from lek centre (quadratic)	0.00±0.00	-1.51	0.130	0.00±0.00	-2.14	0.032
Tip spots	Body mass	0.00±0.00	1.23	0.218	0.00±0.00	-0.06	0.949
	Lyre length	-0.02±0.02	-0.89	0.372	0.01±0.01	0.76	0.445
	Blue chroma	9.92±6.43	1.55	0.122	-4.51±3.68	-1.23	0.220
	Red eye combs	0.23±0.22	1.06	0.291	0.18±0.10	1.71	0.087
Tip spots	Lek attendance	-0.19±3.39	-0.06	0.955	-0.65±0.80	-0.81	0.418
	Fighting rate	0.26±4.55	0.06	0.954	-2.31±1.02	-2.27	0.023
	Distance from lek centre (linear)	-0.03±0.14	-0.22	0.826	0.07±0.04	1.65	0.099
	Distance from lek centre (quadratic)	0.00±0.00	0.36	0.721	0.00±0.00	-2.60	0.009

Table 3: GLMM outputs for the relationship between vane and tip spots and past sexually selected traits in adult black grouse males. Individuals can express traits as 2 years old expressed past sexual signals as juveniles (1 year olds) so are analysed separately from older bird (>2 years old).

		2 years old			**Older**		
Model	**Parameter**	**β±SE**	**Z**	**P**	**β±SE**	**Z**	**P**
Vane spots	Body mass	0.00±0.00	-0.45	0.650	-0.00±0.00	-1.55	0.122
	Lyre length	0.00±0.01	-0.14	0.890	-0.01±0.01	-0.78	0.433
	Blue chroma	11.00±2.81	3.92	<0.001	7.45±5.19	1.44	0.151
	Red eye combs	-0.08±0.09	-0.86	0.388	0.00±0.11	0.08	0.935
	Lek attendance	-0.19±0.61	-0.31	0.758	-0.35±0.73	-0.48	0.629
	Fighting rate	0.48±0.72	0.67	0.506	1.08±0.84	1.29	0.196
	Distance from lek centre	0.00±0.01	-0.15	0.883	0.00±0.01	0.30	0.762
Tip spots	Body mass	-0.01±0.00	-3.73	<0.001	0.00±0.00	-0.58	0.562
	Lyre length	0.01±0.01	1.68	0.093	-0.03±0.02	-1.61	0.107
	Blue chroma	18.55±3.36	5.53	<0.001	9.59±6.32	1.52	0.129
	Lek attendance	1.76±0.91	1.94	0.052	1.88±1.51	1.25	0.211
	Fighting rate	1.04±0.85	1.22	0.221	2.89±1.09	2.66	0.007
	Distance form lek centre	-0.01±0.02	-0.80	0.424	0.05±0.02	2.47	0.014


Tip spots
Vane spots

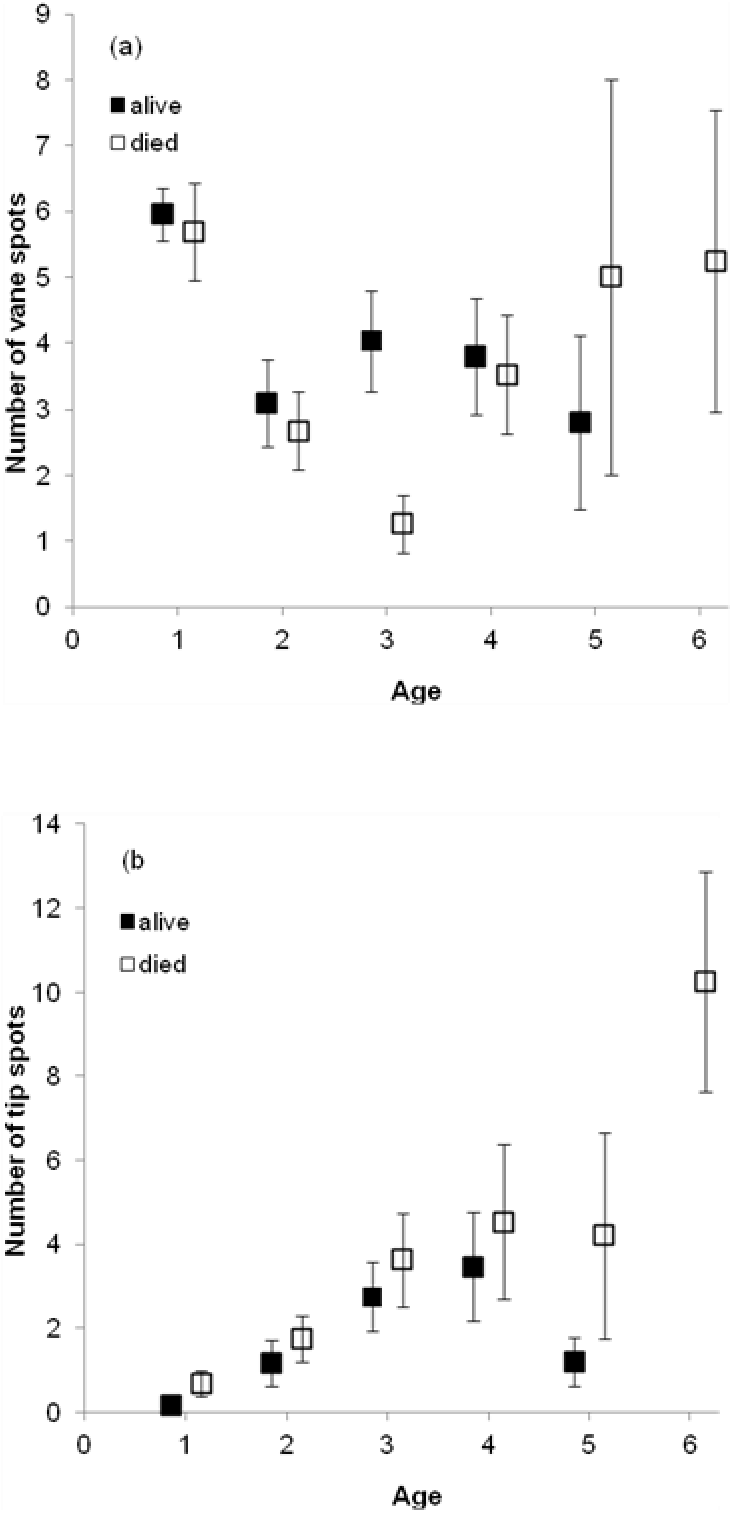

(a)
■ alive
□ died
Number of vane spots
0
1
2
3
4
5
6
7
8
9
Age
0
1
2
3
4
5
6
(b
■ alive
□ died
Number of tip spots
0
2
4
6
8
10
12
14
Age
0
1
2
3
4
5
6

Figure 2

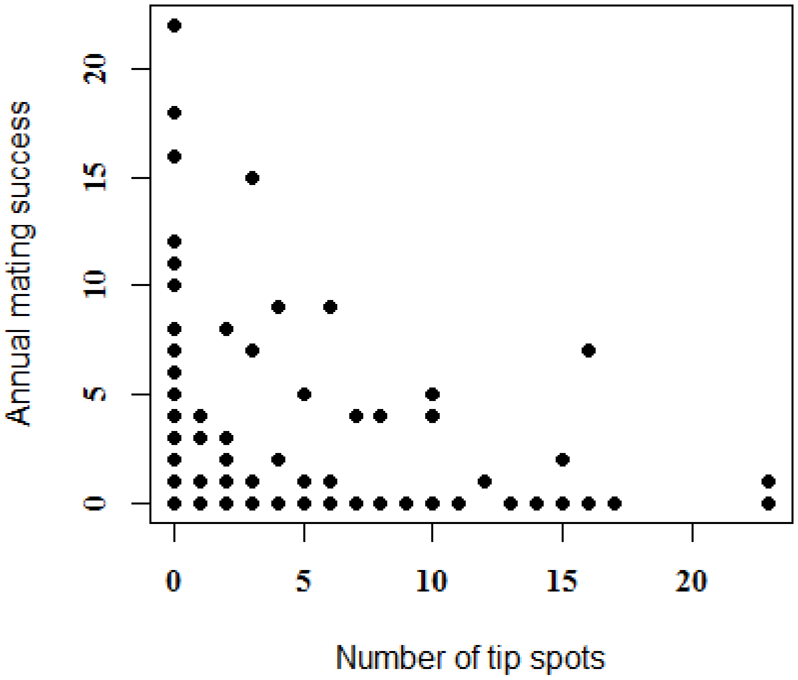
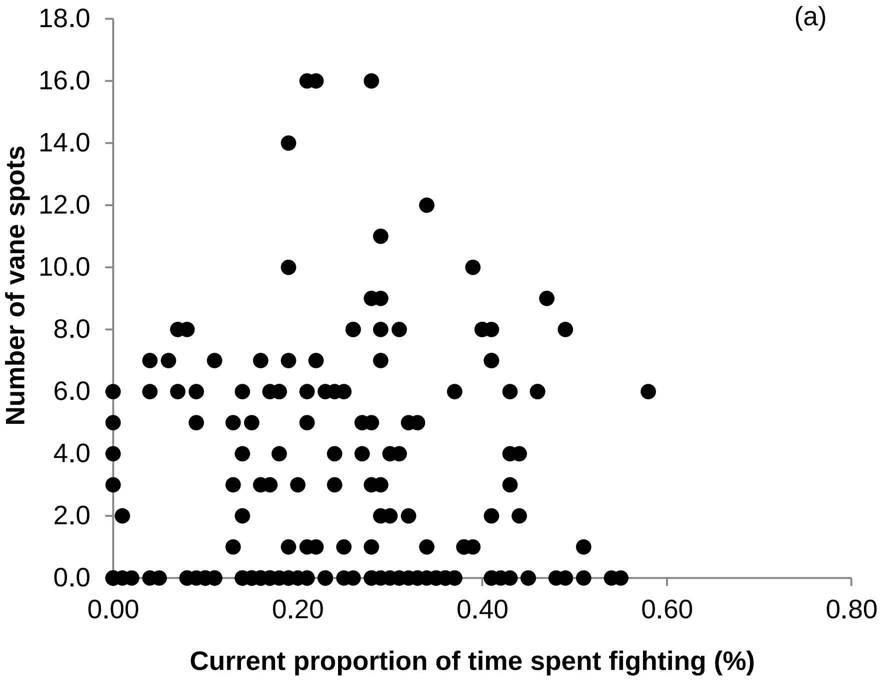
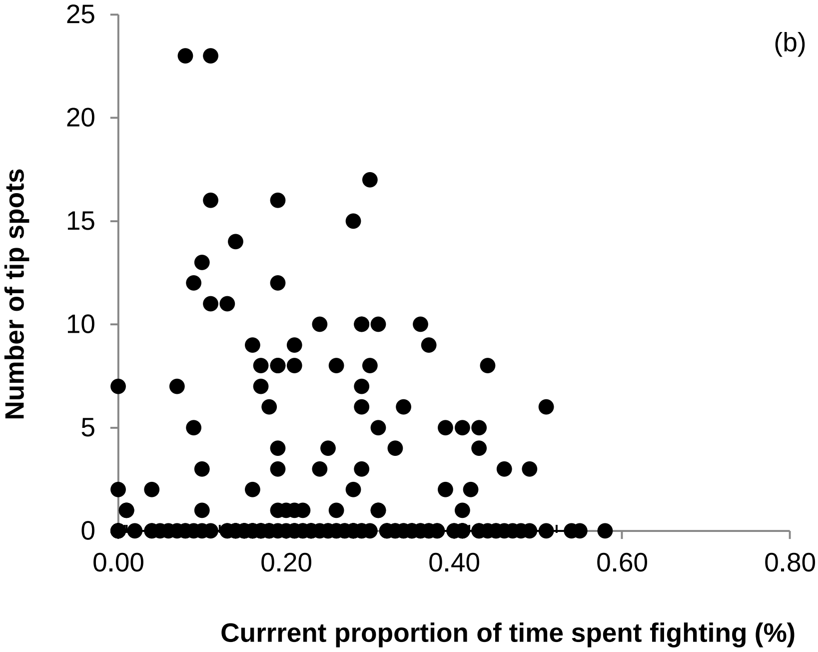

Annual mating success
0
5
10
15
20
0
5
10
15
20
Number of tip spots

Figure 3


(a)
Number of vane spots
18.0
16.0
14.0
12.0
10.0
8.0
6.0
4.0
2.0
0.0
0.00
0.20
0.40
0.60
0.80
Current proportion of time spent fighting (%)

548


(b)
Number of tip spots
25
20
15
10
5
0
0.00
0.20
0.40
0.60
0.80
Currrent proportion of time spent fighting (%)

549

550

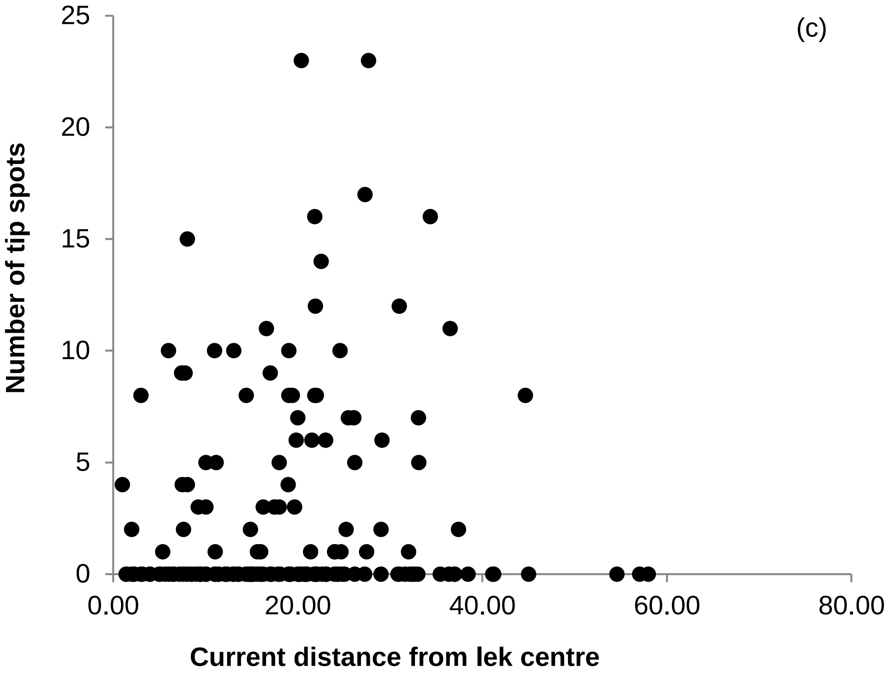

(c)
Number of tip spots
0
5
10
15
20
25
0.00
20.00
40.00
60.00
80.00
Current distance from lek centre

Figure 4

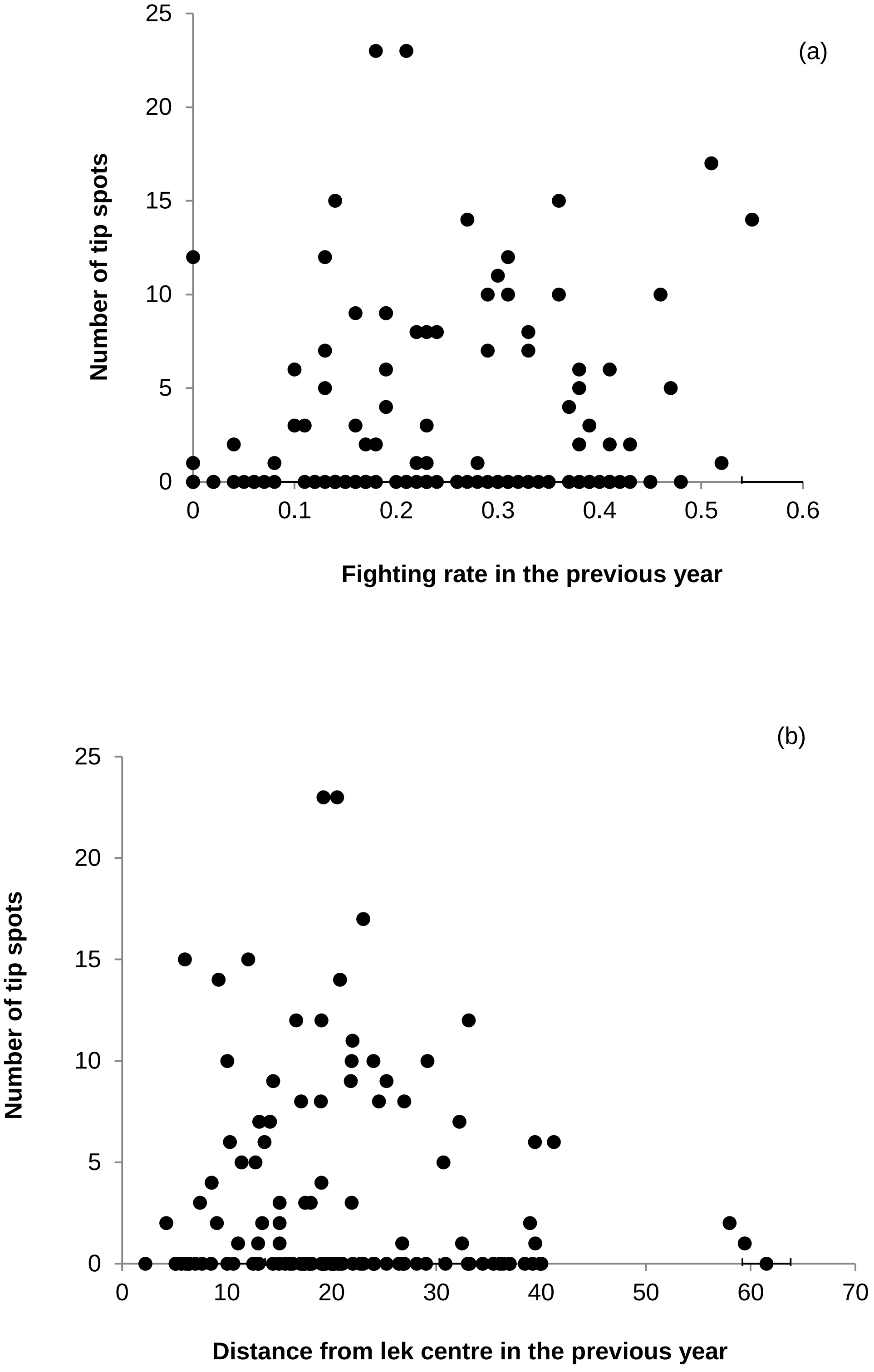

(a)
Number of tip spots
0
5
10
15
20
25
0
0.1
0.2
0.3
0.4
0.5
0.6
Fighting rate in the previous year
(b)
Number of tip spots
0
5
10
15
20
25
0
10
20
30
40
50
60
70
Distance from lek centre in the previous year

Figure 5