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The dynamics of alternative male mating tactics in a population of Black Grouse *Tetrao tetrrix* in the Italian Alps

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Abstract The Black Grouse *Tetrao tetrrix* is primarily a lekking species, although in some populations solitary display is also common. We analysed data from a 25 year-long survey of an increasing Black Grouse population in the western Italian Alps in order to test whether the numbers of males adopting different tactics conformed to patterns expected based on the hypothesis that dominant birds occupy the leks and solitary displaying birds are subordinate, and that the tendency for birds to be excluded from leks increases with lek size. Four predictions were made to test this hypothesis: (i) the proportion of solitary males would increase as the overall population increases, (ii) there would be a threshold at which there is little or no increase in the size of the lekking population, but continued increase in the population of solitary displaying birds, (iii) available lek habitat would be occupied prior to an increase in solitary displaying males, and (iv) there would be an increase in the use of less preferred habitat by solitary displaying males as the total population increases. Population trends varied according to display status in that the lekking population reached an apparent threshold while the number of solitary males continued to increase, and there was an expansion of the range of solitary males into higher altitudes in years when the population was larger. However, there was no increase in the proportion of solitary males as the total population increased. Furthermore, there was no suggestion that suitable lek habitat was limiting, as the number of leks and the mean size of those leks continued to increase throughout the study period. Although two predictions were supported, the precise patterns of trends, and results of additional analyses, suggested that solitary display is more likely to be an alternative rather than a subordinate tactic. Several factors may promote this apparent dual display tactic in Black Grouse, but habitat structure in this and other Alpine populations is likely to be a key influence.

Keywords Density-dependence · Habitat structure · Ideal Free Distribution · Male display · Mont Avic

Introduction

The Black Grouse *Tetrao tetrix* occupies a broad range of habitats throughout its range (Cramp and Simmons 1980), although it is most closely associated with early successional forest stages in Europe (Pearce-Higgins et al. 2007; Watson and Moss 2008). In many regions, populations are declining (e.g. Storch 2000a, 2007; Ludwig et al. 2006; Sim et al. 2008) and it has an unfavourable conservation status in Europe (BirdLife International 2004). The precise cause of the decline is unclear, but may locally include canopy closure, increases in grazing intensity by sheep or deer, increases in nest predation, or climate change (Storch 2000b; Sim et al. 2008). The species is primarily, though not exclusively (Höglund and Stohr 1997), a lekking species, and therefore typically requires some open habitat for display arenas wherein males competitively interact in order to advertise their fitness to females (Alatalo et al. 1992). These may vary greatly in size, with extremely large leks of c. 200 birds being reported (Cramp and Simmons 1980), whilst in other studies smaller leks consisting of a few individuals are more common (Zbinden and Salvioni 2003). Larger leks, which are more attractive to females (Alatalo et al. 2002), are typically traditional sites used year-after-year (Hovi et al. 1996), although there appears to be a lot of variation in mating tactics (*sensu* Lanctot et al. 1998) across areas, with smaller, more ephemeral minor leks being recorded (Alatalo et al. 1992). In some populations, males may also commonly display alone, without any apparent competitive interaction (Zbinden and Salvioni 2003; Höglund and Stohr 1997), whilst in others, there appears to be an 'exploded lek' where widely-spaced males display and interact over relatively large distances (Watson and Moss 2008).

Males that occupy central positions in traditional leks tend to have more copulations, and therefore probably greater fitness, than peripheral males or males in minor leks (Koivisto 1965; de Vos 1983; Alatalo et al. 1992). This may be underpinned by a dominance hierarchy as older males typically dominate traditional leks and occupy the most central positions, hence gaining the most copulations (de Vos 1983), whereas the proportion of first-year males has been reported to be higher on minor leks (Alatalo et al. 1992). It seems likely that, at least for subordinate birds, the display status may be variable within any given year, as birds may spend much of their time away from leks, but nonetheless pay infrequent visits to traditional display sites (Robel 1969). The status of solitary males is generally assumed to be subordinate, as some studies have found them to be mostly first-year birds (Angelstam 2004) with lower mating success (Alatalo et al. 1992), although de Vos (1983) found that, whilst overall copulation rates were lower for solitary males, there were some solitary individuals that achieved high numbers of copulations. Furthermore, Höglund and Stohr (1997) recorded only full adult (rather than yearling) males as solitary displayers, although there were no traditional leks at all on their study site.

There is evidence that the proportions of solitary males may vary over time (Sim et al. 2008) and geographically (Höglund and Stohr 1997, Hancock et al. 1999). This may suggest a degree of flexibility in behaviour, with alternative mating tactics possibly driven by habitat structure (Höglund and Stohr 1997), or by dominance hierarchies and competition for places on lek sites. The latter system may be expected to conform to ideal free distribution (and related) models (Fretwell and Lucas 1970; Milinski and Parker 1991), where the most preferred sites are occupied first, but as the population density increases, competition leads to less preferred sites being occupied (e.g. Höglund et al. 1998). For Black Grouse, the distribution of males on leks has been shown to conform to an ideal free distribution (Alatalo et al. 1992), although this study did not consider solitary males. If dominance dictates whether an individual displays on a lek or as a soloist, then display status can be considered directly analogous to site occupation in ideal free distribution models. A greater understanding of the precise dynamics of solitary males in relation to populations on leks would be of value in developing a better understanding of population change in this species. However, to our knowledge, there has to date been no direct consideration of how changes in solitary displaying males are linked to changes in populations on leks.

In this paper, we analyse data from a 25 year-long survey of an increasing Black Grouse population in the western Italian Alps, including annual monitoring of leks and solitary displaying males. The underlying causes of the population increase are unclear, although they may include climate change and changes in vegetation structure (Bocca 2000). Our general aims were to describe patterns of population change and lek occupancy and to determine whether different patterns of change were evident in the number of male Black Grouse on leks compared to the number of solitary displaying males. More specifically, we assessed the extent to which there was support for the hypothesis that *solitary display is a tactic adopted by competitively inferior individuals who are unable to gain access to leks*, rather than an alternative, although possibly equally successful, display tactic potentially mediated by habitat structure (Höglund and Stohr 1997). This hypothesis is underpinned by density-dependent processes, whereby the tendency for birds to be excluded from leks increases with lek size, and thus predicts: (i) an increase in the proportion of solitary males as the overall population increases, as subordinate birds are unable to maintain a territory amongst more dominant birds on leks; (ii) a threshold at which there is little or no increase in the size of the lekking population, but continued increase in the population of solitary displaying birds; (iii) that available lek habitat will be occupied prior to an increase in solitary displaying males (i.e. that suitable lek habitat is limiting); and, (iv) an increase in the use of less preferred habitat by solitary displaying males as the total population increases. For the latter prediction, we used altitude as a proxy for habitat, assuming that at higher and lower altitudes it becomes progressively less favourable to the species, because Black Grouse is a species which shows a preference for forested areas close to open habitats (Watson and Moss 2008) and is thus strongly associated with treeline habitats in the Alps, occupying a relatively narrow altitudinal range.

Methods

Study site

The research was carried out in Mont Avic Natural Park (Chalamy Valley, Valle d'Aosta, 50°60' N, 3°90' E) in the northwestern Italian Alps; the protected area belongs to the Natura2000 network (Site of Community Importance IT1202020 Parco Naturale Mont Avic, Special

Protection Area IT1202000 Mont Avic and Mont Emilius). The site forms roughly a 'C' shaped ridge at 1400-2250 m a.s.l. which is reasonably self-contained in terms of proximity to likely suitable Black Grouse habitats, being largely surrounded by valleys and higher peaks where Black Grouse are rarely recorded (MB, pers. obs.). The study area of about 2000 ha (Fig. 1) includes forests dominated by Mountain Pine *Pinus montana uncinata*, but also frequent Larch *Larix decidua* and Scots Pine *Pinus sylvestris*, some subalpine pastures, peat-bogs, small lakes and scree slopes. Ericaceae (mostly *Rhododendron ferrugineum*, *Vaccinium myrtillus*, *V. vitis-idaea*, *V. gaultherioides*), Juniper *Juniperus communis*, Green Alder *Alnus viridis*, dwarf Mountain Pines and scattered grassy patches constitute the main understory and also scrub above the treeline. Cattle grazing occurs annually, although the intensity has not changed over the study period. Hunting has been banned within the park since 1989, although it still occurs in the surrounding area, but the pressure is low (MB, unpubl. data).

Black Grouse counts

Every year (1986-2010) the site was monitored at dawn from 25 April to 20 May (the period of maximum display activity) from 39 fixed observation points by a team of trained observers (MB provided the training in each year), one individual for each point, covered in 2-5 sessions carried out within as brief a time period as possible. Counts were only carried out in calm, dry weather, the optimal conditions for display (Baines 1996); if conditions changed during the count, it was abandoned and carried out on the next suitable day. The points were selected based on the view afforded to the surrounding landscape, and the position of points across the site (Fig. 1) was such that virtually all of the site could be seen from the vantage points,

and therefore all likely Black Grouse habitats (for display, foraging or roosting) were surveyed. The observer would position themselves at a given point and record all male Black Grouse seen or heard displaying during the first 90 minutes after sunrise, when most individuals do not move significantly (Cayford and Walker 1991). Each point was surveyed once per year. The precise location was mapped as the point where a male was first observed in display. A lek was defined as any situation where two males were displaying within a maximum distance of 100m from each other, and where there was apparent interaction (in the vast majority of cases, the males were much closer and there were clear interactions between males on leks).

Every male detected was geo-referenced on ArcGIS. In most years, each male was classified according to whether it was displaying on a lek or solitarily. A location where a lek was recorded in at least one year was defined as a lek site. Only total displaying males, and not males according to display class (i.e. lek or solitary), were counted in 1986, 1988-1990, 1992 and 1994-5, so sample sizes were lower ($n = 18$) when considering trends according to display class.

Statistical analysis

Normally distributed data were analysed using GLMs specifying normal errors. Lek occupancy was analysed in relation to the mean number of birds present on the lek over the 25 years of the study (and only including years when birds were present) in order to determine if the leks occupied in more years were larger. The altitudinal range of Black Grouse males (as the dependent variable) per year was analysed in relation to population size, where minimum and maximum altitudes per year were log-transformed prior to analysis. For these analyses, the altitude for each registration was calculated from GIS, and the minimum and maximum altitude was calculated for each year and each display class.

Count data were analysed using GLMs specifying Poisson and negative binomial errors and GAMs. Model performance for these three approaches was compared, the best model being selected on the basis of the lowest AIC (corrected for small sample size) following Zuur et al. (2009). Where $\Delta AIC < 2$ for a given pair-wise comparison, models were considered equivalent (Burnham and Anderson 2002). In such cases, Poisson was always selected over negative binomial models which in turn were selected over GAMs.

The trends in the number of leks, and in male count, were analysed in relation to year, and for the latter, display class (i.e. lek or solitary) specified as a factor. Differences in slope were analysed using the interaction between year and display class (GLM) or fitting separate smooths (GAM; Zuur et al. 2009). In order to assess whether the proportion of solitary displaying males in the population increased as the total

population increased, the number of solitary males was modelled in relation to the total population size, and $\log(\text{total population size})$ was also used as an offset. Where AIC indicated that a GAM was the best model, due to highly non-linear patterns in Black Grouse count, smooths were fitted, specifying a Poisson distribution and using a thin plate regression spline. The optimal degree of smoothing was identified by cross-validation, and a gamma value of 1.4 was specified in order to minimise overfitting (Zuur et al. 2009) and provide a more conservative estimated degrees of freedom (edf), a measure of non-linearity (a GAM with $\text{edf} = 1$ is a straight line). The `glm` (normal and Poisson models) or `glm.nb` (negative binomial models) commands in R were used to fit the GLMs. GAMs were fitted using the `gam` command in the `mgcv` library in R version 2.12.1 (R Development Core Team 2010).

For simple correlations between variables, Pearson's correlation coefficient was used when the data were approximately normally distributed (log-transformations were sometimes necessary). Otherwise, Spearman's rank correlation was used. Means and model parameter estimates are presented ± 1 SE unless otherwise stated.

Results

Trends in numbers of leks and occupancy rates

The number of leks varied from 2 to 13 per year. The lek with the highest mean count contained on average 6.3 ± 0.5 birds ($n = 25$), and was the largest lek in 19 of 25 years. The others were smaller, usually only 2 or 3 birds (Fig. 2), and the next highest mean for years in which the lek was occupied was 2.8 ± 0.5 birds ($n = 10$). There was a significant linear increase in mean size of occupied leks over time (linear regression, $r_{23} = 0.52$, $P = 0.008$, slope = 0.029 ± 0.010). There was a significant, approximately linear increase in the number of occupied leks over the study period (Poisson GLM, $F_{1,23} = 9.22$, $P < 0.006$; Fig. 3). There was a significant positive relationship between population size and the number of occupied leks per year (Poisson GLM, $F_{1,23} = 24.04$, $P < 0.001$, slope = 0.014 ± 0.004). There was also a weaker, but still significant, positive trend between the number of solitary displaying males and the number of leks per year (Poisson GLM, $F_{1,23} = 5.72$, $P = 0.025$, slope = 0.013 ± 0.006). The number of years (out of 25) that lek locations were occupied varied from 3 to 25. Although the largest lek was occupied in every year, there was no overall significant association between mean lek size (when occupied) and the number of years of occupancy (normal GLM, $F_{1,11} = 0.34$, $P = 0.57$) because there were also some small leks which were occupied in all or nearly all years

(Fig. 2). A repeat analysis using maximum instead of mean count produced a similar result ($F_{1,11} = 2.06$, $P = 0.18$).

Trends in count data

The total population of displaying males varied in size between 43 and 92 individuals over 25 years (mean = 69.5 ± 2.9). A GAM fitted to annual counts was selected as the best model (minimum $\Delta\text{AIC} = 5.56$ compared to a Poisson model) and showed a significant ($\chi^2_{4,03} = 55.18$, $P < 0.0001$) and non-linear increasing trend which is illustrated in Fig 4. The overall estimated increase between 1986 and 2010 based on this underlying smoothed trend was 47%. The total deviance explained by the GAM was high at 77.7%.

Over the 18 years for which males were classified according to display status, the size of the lekking population varied between 17 and 39 individuals (mean = 29.0 ± 1.6). The average number and variability of solitary males (46.9 ± 2.0) was greater, although F tests comparing variances between display classes (Zar 1984) showed no significant difference between inter-annual variability of counts in lekking and solitary males ($F_{17,17} = 1.45$, $P < 0.50$). There was no evidence that the proportion of solitary males in the population increased as the total population increased (Poisson GLM, $F_{1,16} = 0.14$, $P = 0.71$).

A GAM with display class as a factor and separate smooths for annual effects provided a better fit than a single annual trend fitted across both display classes ($\Delta\text{AIC} = 2.67$), showing that trend according to display class differed, and hence trends were analysed separately. There were significant effects of year for both lekking ($\chi^2_{3,64} = 14.13$, $P < 0.0051$) and solitary ($\chi^2_1 = 10.26$, $P < 0.0014$) males. The solitary males showed a linear increase, but the trend in numbers of males in leks was non-linear, and in particular the trend exhibited a levelling-off, and even a slight decrease, in numbers on leks as the number of solitary males continued to increase (Fig. 5), although we note that greater caution is needed in interpreting smoothed trends close to the beginning and end of a time series (Zuur et al. 2009). In contrast to the prediction made in the Introduction, there was a significant negative association between the proportion of solitary males in the population derived from the smoothed estimates (Figs 4 and 5) and the smoothed estimate of total population size from year-to-year (Spearman rank correlation $r_s = -0.72$, $P < 0.001$; Fig. 6).

Altitude

In years when the total population size was higher, there was a range expansion to both to higher (normal GLM, $F_{1,23} = 17.98$, $P < 0.0001$, slope = 0.0005 ± 0.0001) and lower ($F_{1,23} = 8.09$, $P = 0.009$, slope = -0.0010 ± 0.0004) altitudes, although the greater significance and lower AIC ($\Delta AIC = 47.10$) suggested that there was a closer relationship with increasing altitude. The overall mean altitudinal range was greater for solitary displaying males (493.2 ± 21.5 m, $n = 18$) than for leks (373.4 ± 15.8 m, $n = 18$). The altitudinal range of solitary males expanded significantly to higher, but not lower altitudes when the overall population size was larger (Fig. 7). The former result was stronger when altitudinal range was related to the population of solitary males ($F_{1,16} = 9.78$, $P = 0.006$). There was no significant expansion of range either to minimum or maximum altitudes for lekking males (Fig. 7).

Discussion

There was no consistent support for the hypothesis that solitary displaying males were subordinate birds unable to obtain a place on a lek due to density-dependent competition. For the four specific predictions given in the Introduction, two were supported: there was an apparent threshold in lekking males at high population sizes, but continued increase in solitary males (prediction ii, Fig. 5), and solitary males, but not lekking males, expanded their altitudinal range (i.e. used less preferred habitat) as the population increased (prediction iv, Fig. 7). However, there was no increase in the proportion of solitary males as the total population increased (prediction i) and no evidence that suitable lek habitat was limiting (prediction iii).

Although two predictions were supported, the precise patterns of trends, and results of additional analyses, suggest that solitary display is more likely to be an alternative rather than a subordinate tactic. The trends in solitary and lekking males differed significantly, and there was a suggestion of a threshold in the lekking population, as predicted (Fig. 5). This could imply that the lekking habitat was 'full', and therefore the only option was for solitary display. However, the number of leks (Fig. 3) and the mean size of those leks continued to increase throughout the study period. Furthermore, the variability in counts of lekking and solitary males did not differ, there was no increase in the proportion of solitary males as the entire population increased, and when considering the smoothed trends, this relationship was negative. This latter result arose due to the increase in lekking males being higher than that of solitary males in the middle part of the study period (Fig. 5 & 6). Furthermore, the smoothed trends suggested that the proportion of solitary males was relatively high during the early part of the study period, when the lekking population was low (Fig. 6). This, in combination with the trend in the number of leks (Fig. 3), clearly shows

that there must have been plenty of suitable lek habitat available in the early period, but despite this, there were still many solitary displaying males. On this basis, the prediction that suitable lek habitat was limiting is not confirmed, and therefore the hypothesis that the solitary male population will show characteristics of occupying less preferred locations must be rejected.

As predicted, there was a significant positive relationship between the range expansion of solitary displaying males and total population size, although this relationship was actually stronger with the population size of solitary males. A random distribution of individuals is likely to result in an increase in range, so this effect may merely be due to population expansion of solitary males rather than habitat use driven by density-dependent processes related to the entire displaying male population. However, there was no equivalent significant expansion to lower altitudes, which would be expected under a scenario of random settlement. Furthermore, a similar process did not occur for the lekking population – despite an increase in population size and an increase in the number of leks, there was no significant increase in the altitudinal range. The implication is therefore that habitat requirements for leks are more restrictive than for solitary males, which accords with the lower habitat thresholds required by solitary compared to lekking males at a landscape scale in Sweden (Angelstam 2004).

Habitat structure may be a major determinant of display tactics, in particular a predominance of solitary displaying when there are no or few open areas (Höglund and Stohr 1997). This may have been an influence in our study area, which was mostly forested (dense evergreen conifers), and open areas were not widespread due to the highest suitable areas being close to the treeline, and even areas above the treeline were often dominated by scrub and scree slopes. Furthermore, there seems to have been an increase in canopy closure and scrub development overtime (MB, pers. obs), a result of long-term successional changes following a steady decrease in grazing in the area between 1960 and 1980. However, this is unlikely to completely explain the overall high rate of solitary display given there was apparently available lekking habitat.

Predation can be the major cause of mortality for Black Grouse (Warren and Baines 2002). Although there is little quantitative data for the study site, there is no evidence that mammal predation pressure (mainly Red Fox *Vulpes vulpes* and Martens *Martes* spp) has increased over the study period (MB, pers. obs.). Avian predators are scarce and there has been no apparent change over time - there have been two Goshawk *Accipiter gentilis* territories in the park and adjacent area more-or-less annually, but no change over time, and the park is within a long-term Golden Eagle *Aquila chrysaetos* territory, although nest monitoring suggests that this pair has very low reproductive success (MB, unpubl. data). Changes in adult predation therefore seem unlikely to have affected the population trend. However, overall predation risk may be relatively low in this population (certainly from avian predators), which could have an influence on

display tactics, e.g. if leks also provide a dilution effect (Hamilton 1971), this constraint may be lifted when predation pressure is low, hence solitary display provides an alternative strategy. A similar effect may have operated if hunters are perceived as predators. Although human disturbance, which may influence display behaviour leading to more solitary displaying males (Zeitler 2000), has been almost absent throughout the period, there was some autumnal hunting at the beginning of the period (up until 1989), which seems to coincide with an upturn in the population. This may have contributed to the overall population increase, although given that some of the lowest counts were recorded in the years immediately after hunting ceased (Fig. 3), this seems unlikely. However, the lack of hunting could have been a contributory factor in the increase in solitary displaying males, if this is linked to a decline in 'predator' avoidance related flocking behaviour

There is the possibility that the local population increased due to increased immigration from other areas, although given that the site is fairly isolated, and that males rarely disperse from the natal area (Caizergues and Ellison 2002; Warren and Baines 2002), this seems less likely for males. However, females are more dispersive and it may be that an influx of females could have influenced overall population trends in males (i.e. more females reproducing in one year could lead to more males in the subsequent year). This in turn could influence display tactics, e.g. a highly skewed sex ratio could mean there are so many females that males don't need to be on a lek to successfully mate. Furthermore, there is evidence that relatedness of males may be important in terms of lek occupancy, where leks are more likely to be composed of related 'tribes', and outsiders are excluded (Watson and Moss 2008). If birds are immigrants, then exclusion from leks by groups of related Black Grouse could also have contributed to the increase in solitary display.

One aspect where this study differs from studies in northern Europe is that the leks were fairly small, although similar in size to other Alpine populations (e.g. Ellison et al 1981; Meile 1982; Marti & Pauli 1983; Scherini et al. 1986; Bocca 1987; Zeitler 2000; Zbinden and Salvioni 2003; Zeiler & Nopp-May 2006). An additional possibility is that the population is made up largely of solitary males that display at a number of relatively small open locations within their home range. When some males happen to meet in an open area, then by our definition a lek is formed. As the population increases, such meetings (possibly of only 2 or 3 individuals) are likely to become more frequent. Hence, if solitary displayers are fairly mobile, even a random distribution will result in the patterns observed. Indeed, Höglund and Stohr (1997), in a population consisting almost solely of solitary displaying males, found that their distribution was no different to random. If leks were selected based on some measure of habitat quality (e.g. openness of habitat, attractiveness to females), then some evidence of preference over time (i.e. the largest leks having the highest rates of occupancy) would be expected. Given that, apart from the largest lek, there was no apparent lek hierarchy (i.e. lek occupancy was not related to lek size; Fig. 2), this random selection seems plausible. The presence of a single apparently 'traditional' lek suggests that alternative tactics do exist in

this population, although it is not clear why this arena differed from other open areas on the study site, but factors additional to habitat, such as relatedness of males or simply tradition itself, may be important.

The survey methods used essentially take an annual 'snap-shot' of the displaying male population, but it seems likely that to some extent display behaviour is flexible within a given year. For example, juvenile males are likely to be more exploratory, and so move around more, and they may engage in both solitary display and lekking display, although visits to leks may be infrequent (Robel 1969). However, we are confident that the trends we have detected are real as we see no reason why there should be any systematic errors in the survey methods which could be confounded with year. A further aspect is that some males may not display at all – we assume here that these are reproductively inactive, so they are unlikely to have a bearing on conclusions, but further intensive work would really be needed in order to determine the proportion of non-displaying males in the Mont Avic population, and how they might influence the dynamics of display tactics.

In this study, we adopted a limit of 100m to define whether displaying birds could be considered lekking or solitary, which was based on the maximum radius at which birds were observed to interact in open areas, i.e. it was defined from a point of view of 'traditional' and relatively small lekking arenas (note that the majority of displaying birds in our survey were clearly displaying together within < 50 m of one-another). Precise definitions of what constitutes a lek or a solitary display in terms of separation distances are rarely given in the literature (e.g. Alatalo et al. 1992; Hancock et al. 1999; Pearce-Higgins et al. 2007), although Hjorth (1970) defined a 50m radius, and Rintamäki et al. (1999) reported an average distance of displaying males from the lek centre in spring as $13.9\text{m} \pm 5.4\text{ SD}$, suggesting our definition covers a relatively large area. However, other authors have used a much looser definition of leks and solitary displaying birds, e.g. de Vos (1983) considered birds to be lekking rather than solitary if they were within 1 km, which is more akin to the concept of an exploded lek (Watson and Moss 2008). This raises the question of whether solitary birds in this and other studies (e.g. Hancock et al. 1999; Zbinden and Salvioni 2003) are in fact interacting with birds on leks. Certainly, auditory signals may be detectable at long distances (up to 3 km, Alatalo et al. 1992), so rather than being a question of solitary versus lek display, it may be more apt to consider the whole system as an exploded lek, which arises due to the relative lack of large open areas of habitat, and where nearest neighbour distance does not significantly influence the chances of males successfully mating.

The population dynamics of southern European Black Grouse differ from those of northern populations, with little or no tendency to cycle and only weak effects of density-dependence (Cattadori and Hudson 1999). Furthermore, the proportion of solitary displaying males is high relative to other studies: up to 74% of displaying males recorded at Mont Avic were solitary (out of a total population of 65 in 1991), a situation

which we believe is probably typical in many Alpine populations (Ellison et al. 1981; Meile 1982; Scherini et al. 1986; Zbinden and Salvioni 2003; Bocca 1987; Celada 1994). Given these differences, we would refrain from suggesting that our findings are likely to apply to other populations of Black Grouse where the population dynamics, habitat, and relative benefits of lekking versus solitary display may be substantially different.

In conclusion, the evidence here clearly suggests that alternative (and possibly equally successful - de Vos 1983) display tactics are being adopted, rather than some birds adopting solitary display as a less-preferred tactic due to competition on leks. The relatively closed habitat of the study area is likely to be important (Höglund and Stohr 1997), although many factors may affect lekking behaviour. Whilst we have speculated on those that might underpin this dual tactic, there is really a need for more intensive studies on marked individuals, including a consideration of the role of females, and preferably genetic studies as have been carried out in more classically lekking populations (e.g. Höglund et al. 1999, 2002), in order to understand the mechanisms underpinning choice of alternative display tactics in Alpine populations of Black Grouse.

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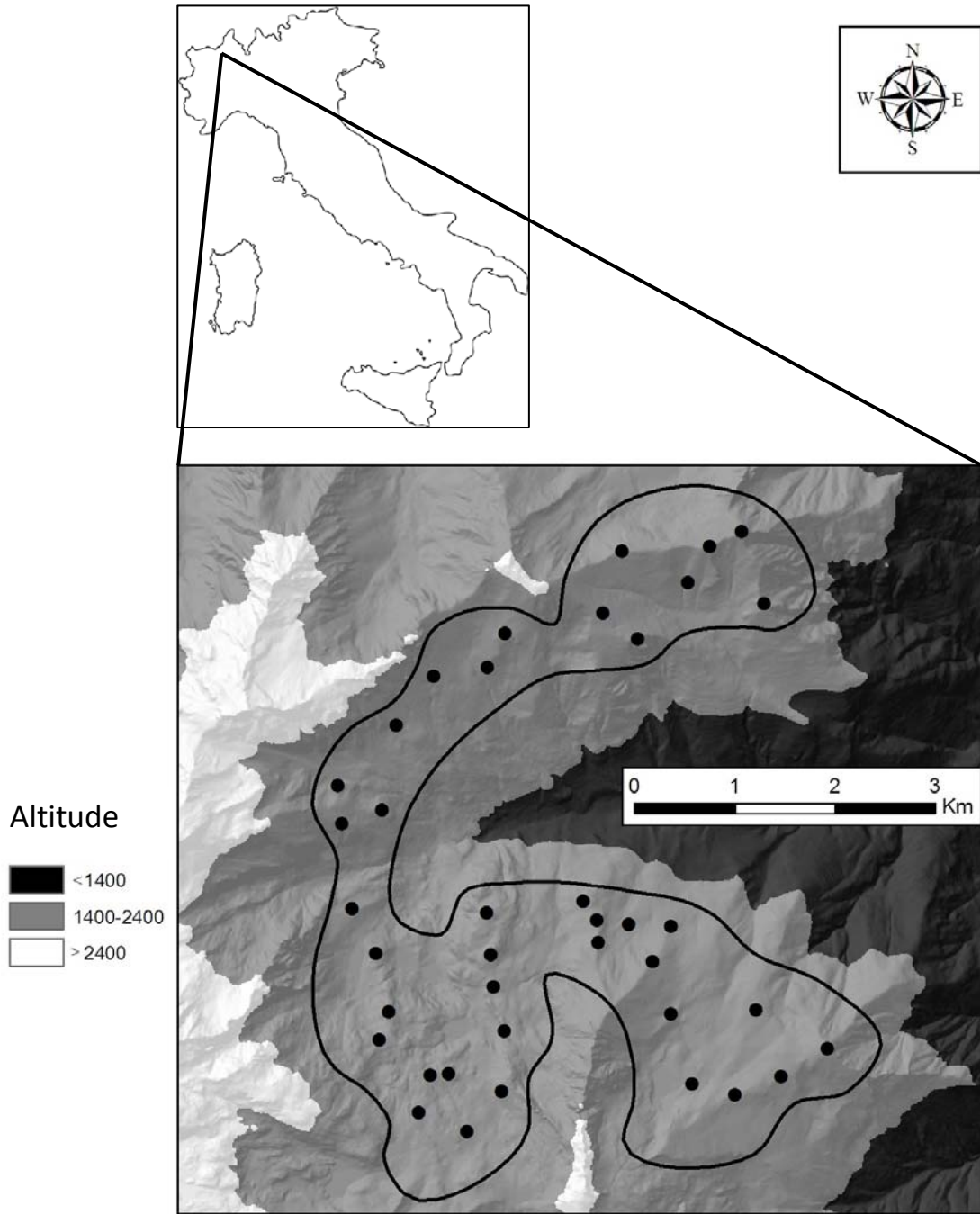


Fig. 1 Map of the study area showing its location in northern Italy (upper panel), and the site boundary and survey locations (lower panel). Black circles indicate the 39 fixed observation points

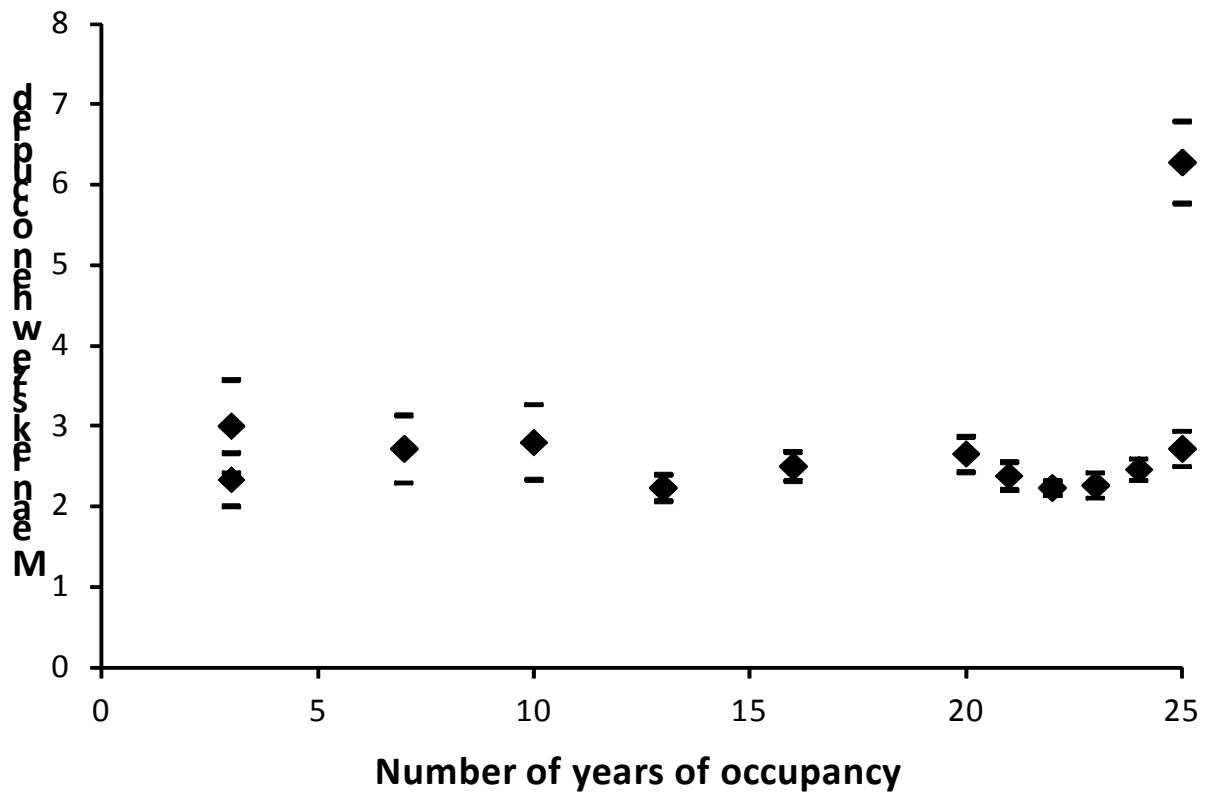


Fig. 2 The mean size of occupied Black Grouse leks in relation to the number of years of occupancy. Bars above and below diamonds represent ± 1 SE

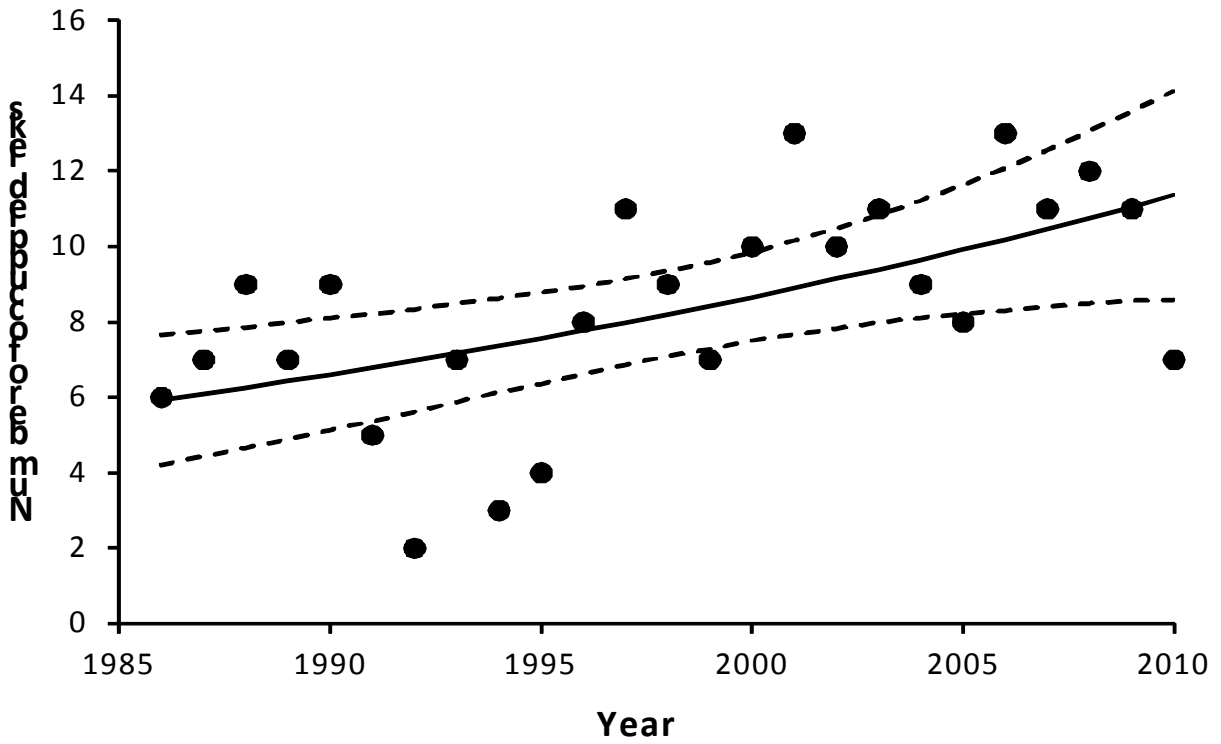


Fig. 3 The number of occupied lek locations per year, where circles are observed values, the solid line is fitted from a GLM with Poisson errors, and broken lines are the 95% confidence interval around the means

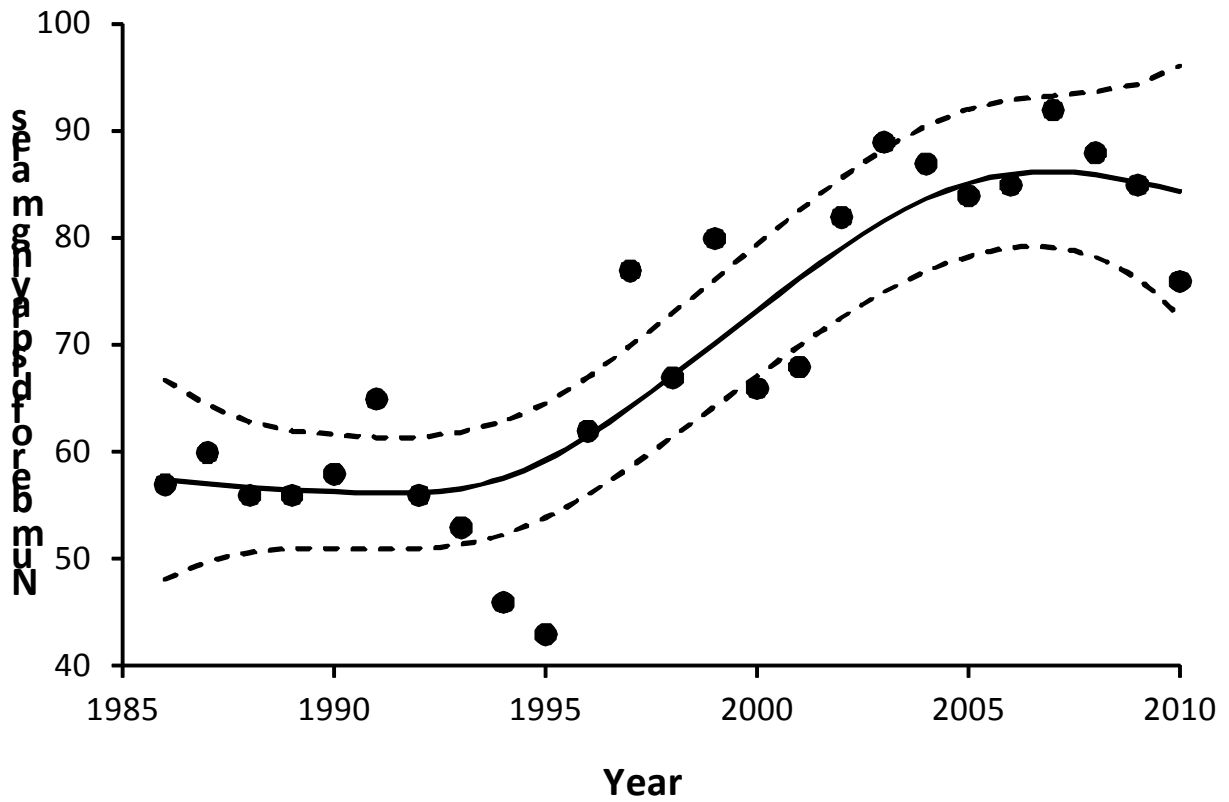


Fig. 4 Black Grouse trend for all displaying males (lekking or solitary) counted per year, where circles are observed values, the solid line is a smooth (edf = 3.25) fitted from a GAM with Poisson errors and an optimum degree of smoothing estimated by cross-validation, and broken lines are the 95% confidence interval around the smoothed trend

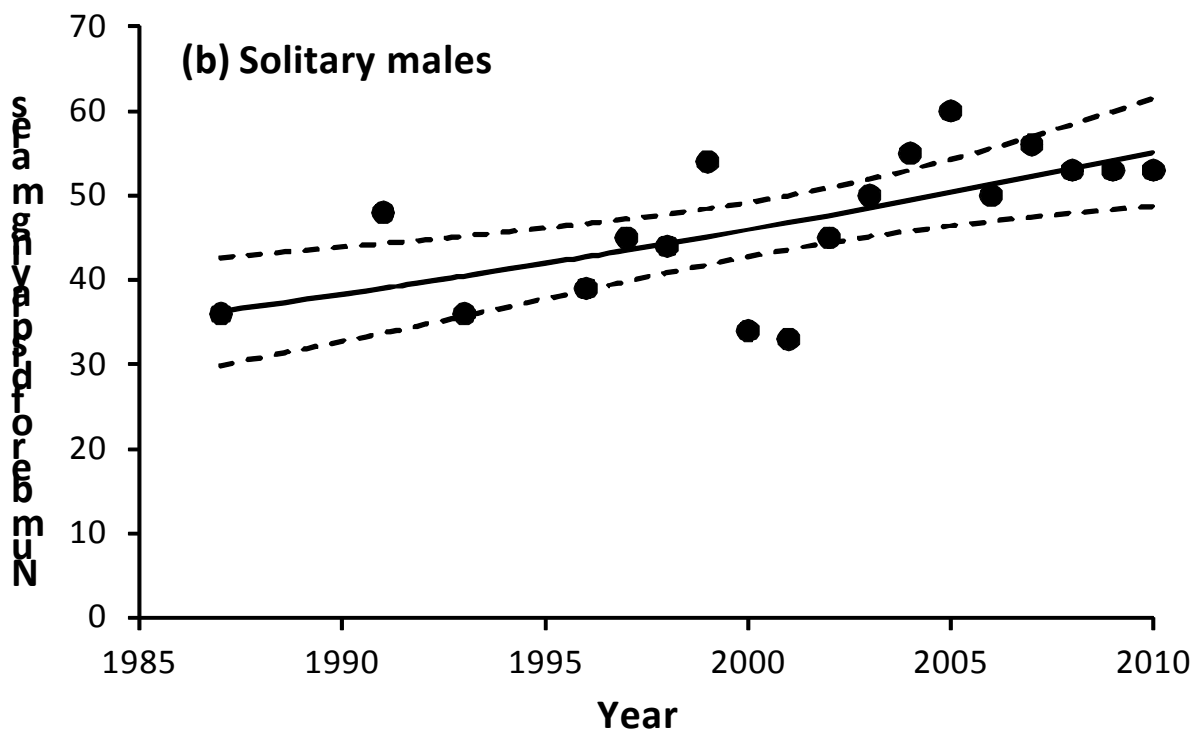
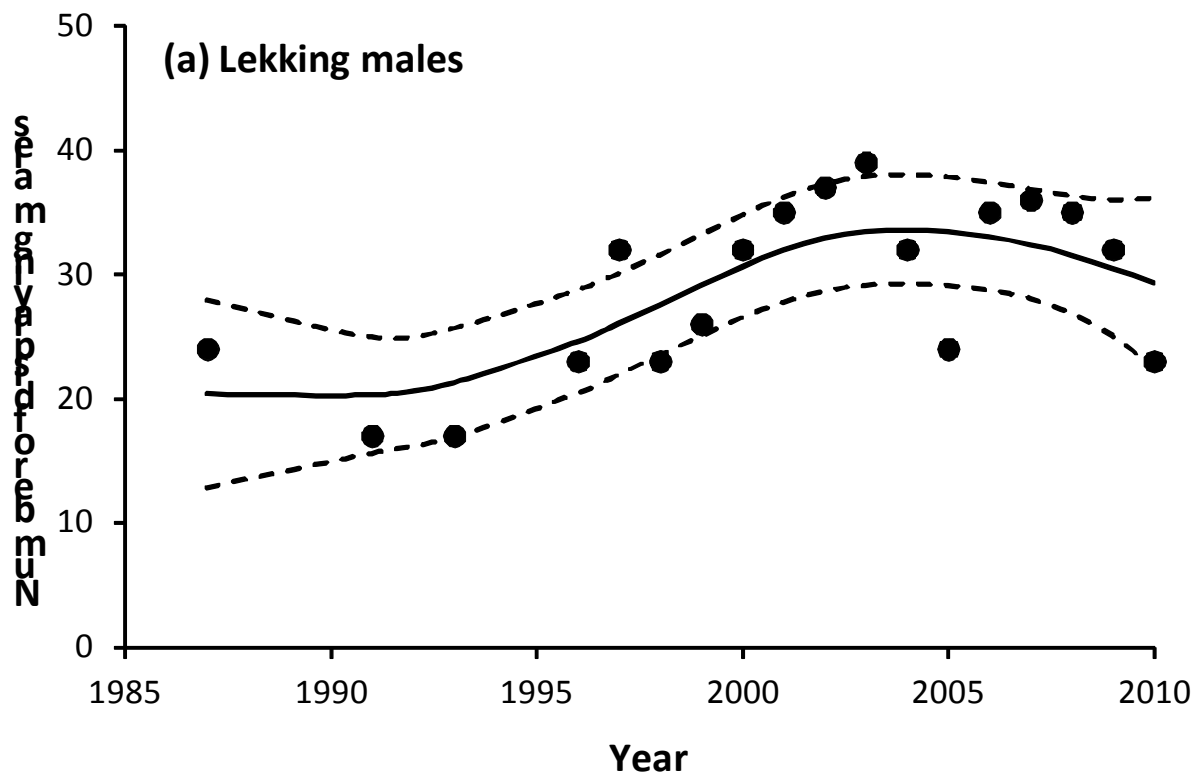


Fig. 5 The number of displaying males per year defined according to display class (lekking and solitary). Smoothed trends (solid lines) and 95% confidence limits (dashed lines) derived from GAMs are presented. edf = 2.92 (lekking) and 1.00 (solitary)

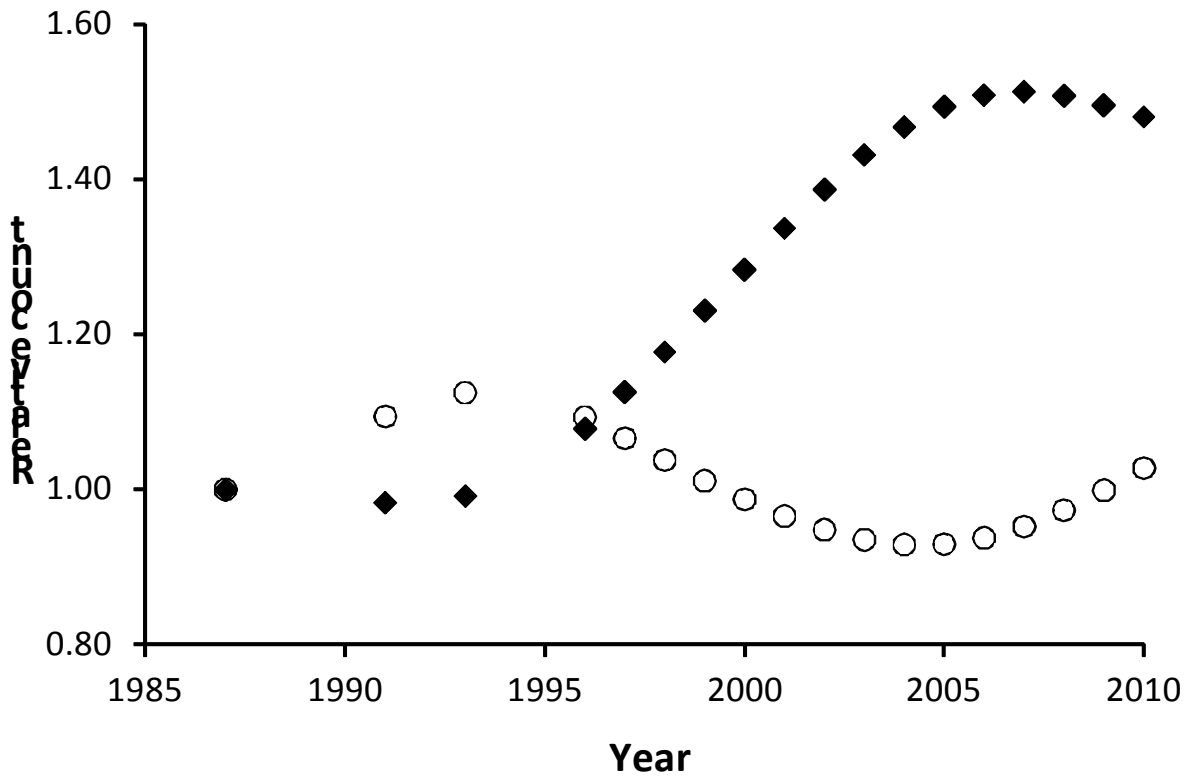


Fig. 6 Smoothed trends of the total population size of displaying males (black diamonds) and the proportion of solitary males in the total population of displaying males (white circles). Both trends have been expressed relative to the first year of the time series (set at 1)

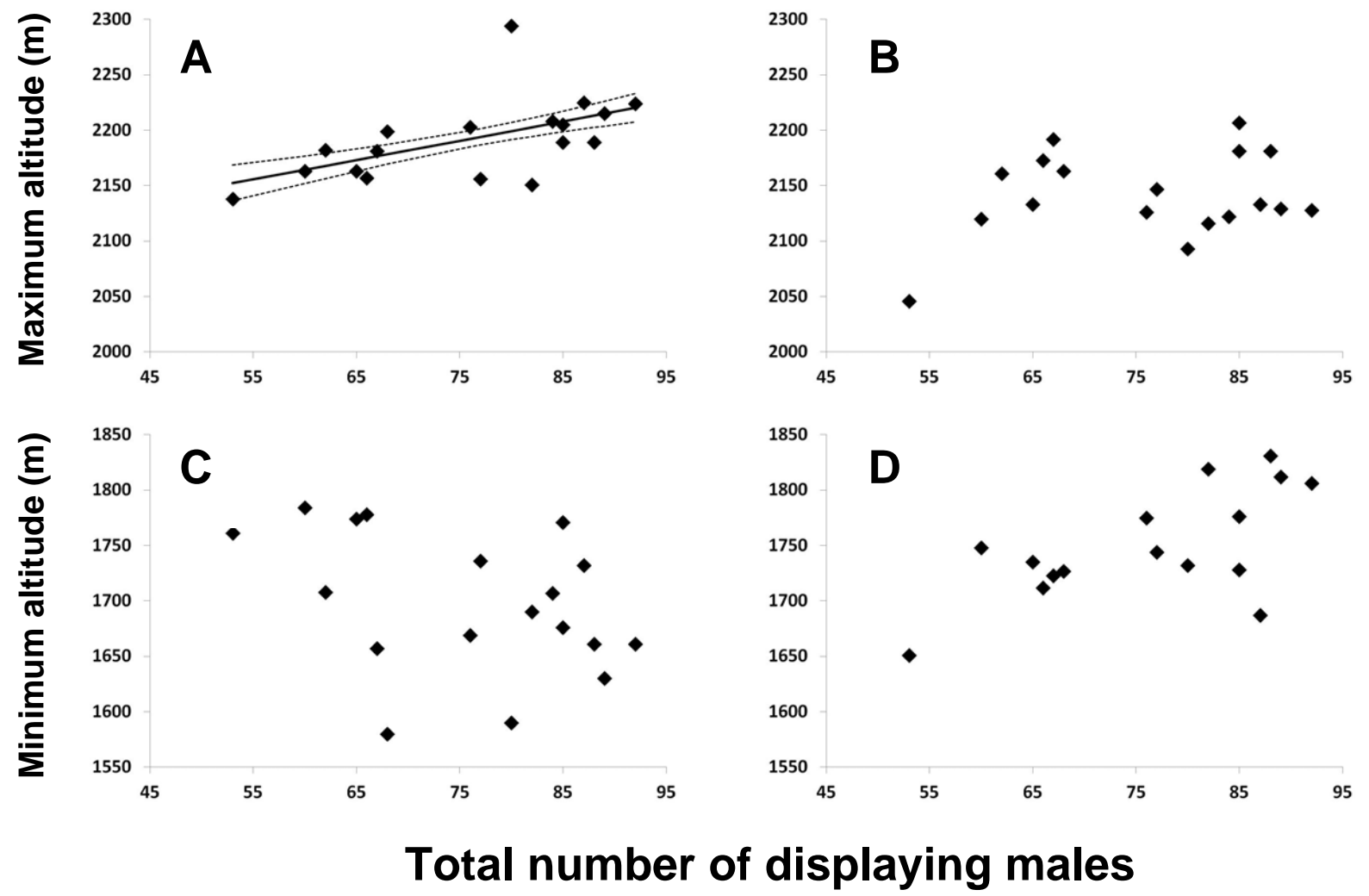


Fig. 7 The maximum and minimum altitude (m) of lekking and solitary displaying males in relation to the total number of displaying males per year. Regression lines (solid lines) and standard errors (dashed lines) derived from linear regression are given when significant (normal errors GLM). Note that the original regression coefficients are $\log(\text{altitude})$ – estimates in this graph have been back-transformed. A Solitary males, maximum altitude ($F_{1,16} = 7.39, P = 0.015$); B Lekking males, maximum altitude ($F_{1,16} = 1.04, P = 0.32$); C Solitary males, minimum altitude ($F_{1,16} = 2.56, P = 0.13$); D Lekking males, minimum altitude ($F_{1,16} = 2.76, P = 0.11$).