# Are nonsocial species more social than we think? Seasonal patterns in sociality in a solitary terrestrial carnivore

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## ARTICLE INFO

Animal sociality, the extent and manner in which conspecifics associate with each other, ultimately affects an individual's survival and reproductive success. It is shaped by the spatiotemporal configuration and composition of the social units (e.g. individual, pair, group) in a population. Here, we assessed the formation and structure of social networks of a presumed nonsocial species with individual-based movement data of 153 GPS-marked brown bears, *Ursus arctos*. We explored changes in the frequency of dyadic associations in relation to distinct seasonal patterns (i.e. mating, hyperphagia and hunting seasons) that affect bear behaviour. We found seasonally distinctive frequencies in brown bear associations throughout their active period and that reproduction was the main driver for associations in the population, that is, the highest frequency of associations occurred during the mating season and male–female dyads during the mating season included the majority (73%) of observed associations. We also observed dyadic associations during the hyperphagia and hunting seasons, but found no significant changes in frequency during these seasons. In addition, we found that social structures during both the mating and nonmating periods were nonrandom, that is, dyadic associations occurred more often than expected. Animal sociality is commonly viewed as a classification of social versus nonsocial, but our results suggest that it is rather a dynamic continuum primarily influenced by variation in a species' spatiotemporal configuration (i.e. seasonal movements, social unit structure) and demographic composition (i.e. age, sex). Our results also support the contention that studies focusing on animal sociality should include a sociospatial perspective, as both components are tightly linked. Since sociality can affect individual fitness, and vice versa, advancing the knowledge on assumed 'solitary' species is paramount for the conservation and sustainable management of their populations.

Animal sociality is driven by ecological and evolutionary processes (Alexander, 1974; Webber & Vander Wal, 2018). Individuals adapt their sociality in response to species' characteristics and environmental conditions (Van Der Post et al., 2015). Sociality is often defined as the extent and manner in which conspecifics associate with each other (Hinde, 1976), and these interactions ultimately affect an individual's survival and reproductive success (West-Eberhard, 1983). It is shaped by the spatiotemporal configuration and composition of the social units (e.g. individual, pair, group) in a population (Kappeler, 2019; Webber & Vander Wal, 2018), and social and movement behaviour can reinforce each other (Webber et al., 2023). For example, group-living species benefit from associating with conspecifics due to increased safety and easier access to resources which, in turn, increase fitness (Clutton-Brock, 2021; Macdonald, 1983). In contrast, solitary species generally benefit from avoiding conspecifics, except during reproduction (Sandell, 1989).

Conspecific associations can be classified as direct or indirect and as affiliative or agonistic (Silk et al., 2013). Direct associations are commonly defined as two or more individuals physically

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meeting, while individuals do not meet during indirect associations but remotely sense and are aware of one another, for example through an existing 'scent-scape' or by sound (Allen et al., 2015; Kashetsky et al., 2021; Vogt et al., 2014). Additionally, either direct or indirect associations can lead to affiliative or agonistic interactions, that is, individuals are attracted to or deterred by conspecifics (Fischer et al., 2017), and create relationships in a population (Hinde, 1976). All types of associations define the sociality of a species, that is, agonistic and indirect associations are likely as important for the sociality of a species as affiliative and direct associations (Firth et al., 2017).

The movement behaviour of animals is generally affected by the distribution of resources such as food or mates, and sociality is therefore likely influenced by the same factors (Webber et al., 2023). For example, hyperabundant food resources may induce solitary species to increase their gregariousness (Elbroch et al., 2017; Wirsing et al., 2018). Reproduction requires almost all species, independent of their gregariousness, to associate with potential mates and is a significant driver of both movement and social behaviour. Additionally, movement of wildlife can be altered by human presence (Fahrig, 2007; Proctor et al., 2023) and periods with high human activity and disturbance (e.g. hunting) can also affect the social dynamics within populations (Cassidy et al., 2023; Swenson et al., 1997; Williams & Lusseau, 2006). Therefore, the sociality within populations, for both group-living and solitary species, might not be a classification of social versus nonsocial, but rather a dynamic process, especially when taking into account that these aspects (food, mates, human activity) are occurring at restricted periods of the year (Sandell, 1989).

By utilizing social network analyses (SNA), a powerful approach to describe and investigate social aspects in a population (Farine & Whitehead, 2015), we quantified the sociality of a solitary and nonterritorial species, the brown bear, *Ursus arctos*. Further, we examined the level of social network structures (e.g. general relationships and patterns between the individuals) at the population level in Scandinavia. The brown bear is a solitary large carnivore and is considered 'nonsocial', that is, it associates for mating purposes but otherwise associates little with conspecifics, except for mothers with dependent offspring (Steyaert et al., 2012) or when individuals in some populations aggregate at locations with hyperabundant food resources (e.g. rivers with spawning salmon or rubbish dumps; Stonorov & Stokes, 1972) especially during hyperphagia, the season when bears feed extensively in preparation for hibernation (Humphries et al., 2003). Brown bears have a polygamous mating system and the mating season lasts from approximately May to July (Steyaert et al., 2012, 2020). Brown bears are nonterritorial (i.e. do not defend a territory), unlike most other large carnivores (Kleiman & Eisenberg, 1973). They show extensive inter- and intrasexual home range overlap, and their general movement patterns are typically linked to the availability of resources, such as food and mates (Steyaert et al., 2012). Many brown bear populations are hunted, which has profound effects on their movement behaviour, mating system and social structures (Frank et al., 2021; Hansen et al., 2022; Leclerc et al., 2017).

The main aim of this study was to assess the formation and structure of social networks of a presumed nonsocial species and investigate the influence of dynamic temporal aspects. We used long-term individual-based movement data of 153 GPS-marked brown bears in south-central Sweden to construct dyadic associations and annual as well as seasonal social networks. We explored changes in the frequency of dyadic associations in relation to distinct seasonal patterns in brown bear behaviour (i.e. mating, hyperphagia, hunting). We investigated three alternative hypotheses to explain the frequency and seasonal distribution of associations in this nonterritorial and solitary species. First, we expected

reproduction to be the main driver for conspecific associations and predicted (1) that associations would be more frequent during the mating than the nonmating season. Second, because hyperabundant food resources cause individuals in some bear populations to tolerate other conspecifics in close proximity (Egbert et al., 1976; Sellers & Aumiller, 1994; Wirsing et al., 2018), we hypothesized that food is the main driver for associations and predicted (2) that association frequency would increase during hyperphagia. Third, human disturbance can cause species to change their movement patterns and habitat use (Lewis et al., 2021) and is likely forcing individuals into the same areas which could possibly lead to an increase in conspecific associations. Therefore, we hypothesized that hunting is the main driver for associations and predicted (3) that association frequencies would increase during the hunting season. Currently, there are no indications for specific fitness benefits linked to social associations outside the mating season for solitary species (Makuya & Schradin, 2024; Sandell, 1989). For brown bears in Scandinavia, there are indications that there is limited aggression between adult conspecifics (Hansen et al., 2022; Støen et al., 2005) and as bears are mainly focusing on an abundant food resource outside the mating season (e.g. berries) and show individual variation in scavenging behaviour (Ordiz et al., 2020), food competition-induced associations are unlikely. Accordingly, we predicted (4) that brown bears should associate with conspecifics nonrandomly during the mating season but outside the mating season associations should be random (i.e. hyperphagia and hunting). Here, 'randomness' refers to any significant changes in occurrence and frequency of associations between the observed network in comparison to randomized networks (Spiegel et al., 2016) on a population level.

## METHODS

### Study Area and Population

The study area is approximately 13 000 km² located in south-central Sweden (61°N, 15°E) and is characterized by bogs, lakes and managed coniferous forests. See Martin et al. (2010) for more information about the study area. All bears in this study were captured as a part of a long-term project on brown bear ecology in Scandinavia. The Scandinavian brown bear population is distributed across most parts of Sweden and in Norway along the border with Sweden, Finland and Russia (Swenson et al., 1995). Bears are darted from a helicopter using a remote drug delivery system (DanInject, Børkop, Denmark) and GPS-collared (GPS Plus; Vectronic Aerospace GmbH, Berlin, Germany) on an annual basis. See Ethical Note below and Arnemo and Evans (2017) for more details on capture and handling. The GPS collars were programmed to relocate the individual every hour. The weight of the collars never exceeded 2% of the bodyweight of the bear (Ordiz et al., 2012). The collars do not have a break-away mechanism as the projects opts to recapture individuals the following year to study bears for multiple years. The population density in the study area is ~23 individuals per 1000 km² (Bischof et al., 2019). The number of marked individuals per year is approximately 50–70% of the local population (Solberg et al., 2006). Brown bears in Sweden are legally hunted from 21 August to 15 October or until quotas are filled, and around 10% are harvested from the total population annually (Bischof et al., 2019).

### Ethical Note

The Scandinavian Brown Bear Research Project (SBBRP) follows a strict and tested capture protocol (Arnemo & Evans, 2017) which has been approved by the appropriate Scandinavian authorities.

The SBBRP has carried out more than 3000 captures since 1984 (Hertel et al., 2019), and the capture-related mortality rate is <2% (Arnemo et al., 2006). All captures are carried out from a helicopter shortly after bears emerge from their winter dens (usually during the middle towards the end of April) to avoid overheating due to high ambient temperatures. The time between first sighting of a bear until darting is usually around 15 min and never exceeds 30 min (Fahlman et al., 2011). All bears are immobilized with a mixture of 2.5 mg of tiletamine, 2.5 mg of zolazepam and 0.02 mg of medetomidine per kg body mass (Kreeger et al., 2023). This dosage and drug combination is well tolerated by healthy bears (Arnemo & Evans, 2017). After immobilization, the bear's eyes are immediately covered to avoid stressful light stimuli, and intranasal oxygen supplementation is routinely administered to avoid hypoxemia. Bears are constantly monitored during anaesthesia, including heart rate, oxygen saturation, breathing and body temperature. Biological samples taken include a circular sample of surface tissue (diameter 6 mm) extracted with a sterile dermal biopsy punch from an ear for genetic analysis, and a vestigial premolar tooth from all bears not captured as a yearling to estimate age based on the cementum annuli in the root (Mattson's Inc., Milltown, MT, U.S.A.). After all measurements, sampling procedures, GPS collaring and other handling is finished, atipamezole is used as an antidote to counter the anaesthetic effects of the medetomidine (5 mg per 1 mg of medetomidine; Kreeger et al., 2023). After the antidote is administered, bears are observed from a safe distance on the ground until movements indicate that the bear is about to safely leave the site. If a bear cannot be safely observed from the ground, we leave the site with the helicopter but return later to observe the bear from high in the air to ensure it is safe. In addition, we intensively monitor GPS locations of recently captured individuals the first few days after a capture to make sure the bear behaves normally. All procedures during capture and handling as well as the follow up after capture are carried out by trained and certified personnel and an experienced team of wildlife veterinarians (Arnemo & Evans, 2017). The project has never found evidence of behavioural or detrimental effects of collars in this population. All aspects of animal capture and handling were approved under an ethical permit by Uppsala Ethical Committee on Animal Experiments (Dnr 5.8.18-03376/2020). Our capture permit was provided by the Swedish Environmental Protection Agency (NV-01278-22).

*Bear Movement and Associations*

We used relocations from 153 GPS-collared bears (453 bear-years) during their active period (i.e. excluding hibernation) from April to October 2003–2022. We focused on males and females ≥3 years, as this is the youngest recorded age for reproduction in both sexes in Scandinavia (Steyaert et al., 2012; Zedrosser et al., 2007). To determine whether bears were associating with each other, we calculated all pairwise distances between all individual bear GPS relocations at a given time rounded to the nearest hour and repeated this procedure every hour ('spatsoc'; Robitaille et al., 2019). We defined an association as two or more individuals that were within a Euclidean distance ≤200 m of each other at the same time based on a natural break analysis (Fig. A1). As the median step length (1 h fix rate only) of brown bears is 517 m for males and 382 m for females (Fig. 1a), it is reasonable to assume that the two individuals could have met physically within a 200 m threshold. To investigate the influence of different distance thresholds on the structure of the social networks, we also compared results using
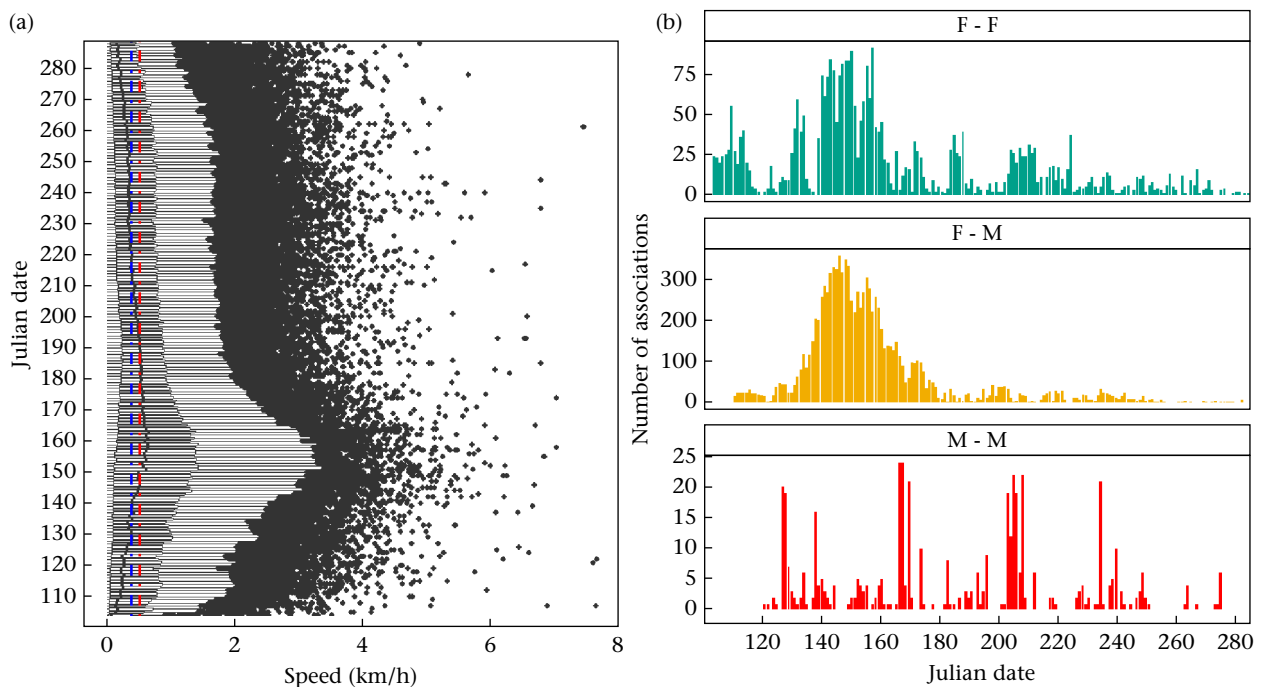


**Figure 1.** The (a) average movement speed (km/h) and (b) frequency of associations per composition of sexes in dyads (200 m threshold) calculated by using GPS data from brown bears in south-central Sweden (2003–2022). For (a), the movement speed was calculated by step length divided by time interval (1 h fix rate only) for all steps from every active individual on a given day. The horizontal lines in the box plots correspond to the median speed during that day of the year, the boundaries are the first and third quartiles, the whiskers are the 10th and 90th percentiles and the points are outliers. The blue and red dotted lines correspond to the median speed of females (382 m/h) and males (517 m/h) respectively. Dates are Julian and encompass the active period of brown bears (i.e. excluding hibernation). For (b), the y-axis varies per dyad composition. F–F: female – female dyads; F–M: female – male dyads; M–M: male – male dyads.

100 m and 500 m thresholds. All data handling and analyses were executed in R 4.3.0 (R Development Core Team, 2023).

To identify distinctive changes in the association frequency in brown bears, we performed a structural break analysis (SBA; 'struccchange', Zeileis et al., 2001) using the associations data set. To investigate whether the different sex compositions of associations showed different patterns, we executed the analysis using the complete data set including all associations but also using a selection of associations based on the sex of the participating individuals (F-M, M-M and F-F). We identified temporal breaks in association frequency, that is, periods of low and high association frequencies. Once these periods were identified, we investigated whether they overlapped with biologically meaningful seasons identified by prior studies in our study area: the mating season from 1 May to 31 July; the hyperphagia season from 1 August to 30 September; and hunting season from 21 August to 15 October. We defined the mating season based on the timing of oestrus in our study population (Spady et al., 2007) and confirmed this with earlier studies (Dahle & Swenson, 2003; Steyaert et al., 2012). The period of hyperphagia largely depends on the ripening of berry species, which is between August and October in our population (Stenset et al., 2016). In Sweden, the hunting season for brown bears is between mid-August and mid-October (Bischof et al., 2008).

The first step in the SBA approach is to determine breakpoints, which can be done by adjusting frequency data into a time series format and computing the most optimal segmentation using a null hypothesis model ('breakpoints' function in 'struccchange' package). The optimal number of breakpoints can be determined with an information criterion-based model selection (Zeileis et al., 2003, 2010). Additionally, the model will also provide the 5% and 95% confidence intervals for all breakpoints. The most optimal number of breakpoints can be used to fit an uninformed regression model, which can be compared to other models using regression model selection approaches. We defined seven candidate models including all possible combinations of the seasons, that is, mating, hyperphagia and hunting season, which had fixed breakpoints, and an uninformed model which was not restricted by any dates but where the breakpoints were determined by the first step of the SBA. We used the second-order Akaike's information criterion (AICc), to correct for small sample sizes, calculated using 'AICcmodavg' (Mazerolle, 2023). We identified the most parsimonious model using a threshold of $\Delta$AICc < 2 to determine the best-supported model (Burnham & Anderson, 2004). Models with AICc values within the set threshold were investigated regarding uninformative parameters, and conclusions were made accordingly (Arnold, 2010).

*Annual Social Networks*

We used a social network analysis (SNA) to compare observed and random network metrics and tested whether associations of individual bears during the entire active period or during the mating or nonmating season (e.g. hyperphagia, hunting) occurred randomly or nonrandomly. SNA was applied to data from 2008 to 2014 (24–36 individuals per year), as the density of GPS-collared individuals was sufficient to create robust social networks (Brask et al., 2021).

To test whether the observed networks were different from random networks, we performed prenetwork data permutations using the method proposed in Spiegel et al. (2016) by maintaining the same spatial overlap between the individuals to omit implausible associations within the random populations. The home range and spatial overlap of all individuals thus remained the same; only the daily movement trajectories were randomized (999 iterations), for example the movement trajectory of a bear on day 1 in the observed network will be assigned to day 10 in one of the randomized networks and day 2 could be assigned to day 25, etcetera. As we maintained the explicit space use of all individuals, we were able to compare the occurrence of dyadic associations between the observed network and randomized networks. We only retained individuals in the analysis with data from all three predefined seasons during a given year, and, in addition, we removed individuals that did not actively participate in the GPS-collared population (i.e. no home range overlap with any other individual based on 100% minimum convex polygons) or showed long-distance movements representing dispersal from the study site (Hansen et al., 2022). We used the 'spatsoc', 'asnipe' (Farine, 2013) and 'igraph' (Csárdi & Nepusz, 2006) packages to create both observed and random networks, and to retrieve network metrics. We used the three distance thresholds to identify associations and investigated the effect of potentially indirect associations (i.e. individuals not physically meeting) on the annual and seasonal social networks. The networks were created and weighted by using the simple ratio index (SRI; Hoppitt & Farine, 2018), calculated as the ratio of unique dyads within the distance threshold divided by the total number of relocations per individual. By using the SRI, we also account for missing observations (Hoppitt & Farine, 2018; Webber & Vander Wal, 2019). For all networks, we calculated two network metrics: the network 'density', defined as the ratio between observed edges and all potential edges in a network, and the 'mean weighted strength', defined as the average individual association index, based on the SRI (Farine & Whitehead, 2015). These metrics have been shown to be correlated with the density and frequency of social interaction within the population (Farine & Whitehead, 2015), where high density values indicate a high number of unique dyads, and high frequency values suggest a high number of associations in a population. Both the observed network metric values are compared to the distributions of the random networks (Farine, 2017; Hobson et al., 2021). When the observed metric deviates from the distribution (> 95% confidence interval), the associations within the social network are nonrandomly structured, indicating a high potential for realized animal 'motivations' (Sharma et al., 2023; Spiegel et al., 2016).

## RESULTS

*Associations and Structural Break Analysis*

We identified a total of 13 738 dyadic associations from 2003 to 2022 using the 200 m distance threshold. The percentage of bears associating with GPS-collared conspecifics was around 3.4% during mating and 0.4% outside the mating season, based on the total amount of GPS positions during the corresponding periods. Brown bears associated with conspecifics throughout their active period with pronounced fluctuations across seasons (Fig. 1b). The most common associations during the active period were between a male and a female ($N = 10 057$), with a peak during mid-May until mid-July (Fig. 2). Same-sex associations (M-M: $N = 470$; F-F: $N = 3211$) were also observed throughout the active period, but in much lower frequencies than among opposite-sex dyads (Fig. 1b).

Based on the SBA, we found that three breaks fitted the association frequency best (Fig. A2). Furthermore, the uninformed model was the most parsimonious (Table 1) in describing the periods of high and low association frequencies for both male–female and same-sex dyads (Tables A1–A3). Female–male associations culminated between the end of May and the beginning of June, male–male ones in June–July and female–female ones between the end of May and the beginning of June. Further, among the best-fitting candidate models with predefined seasons, the majority of
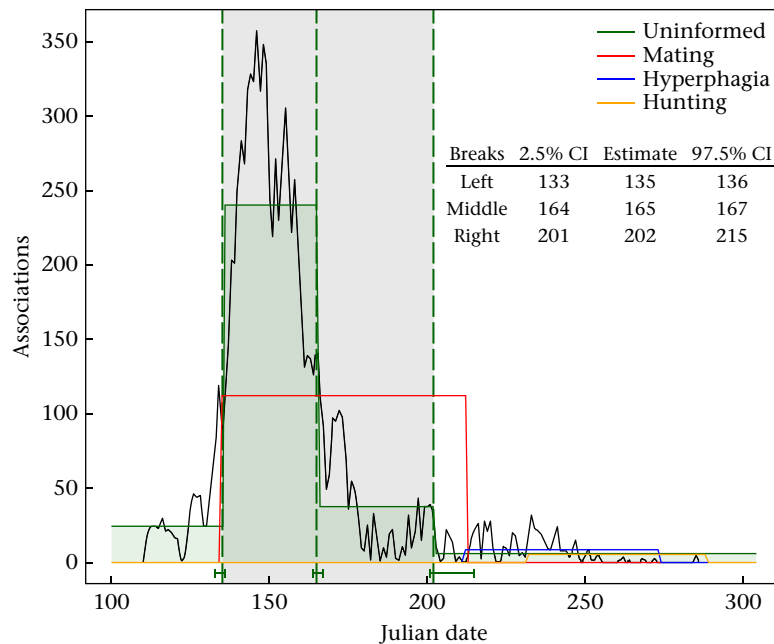
**Figure 2.** Time series plot showing the frequency of associations during the year (Julian date) by female–male dyads based on GPS data from brown bears in south-central Sweden (2003–2022). The lines are the output of the SBA models regarding the uninformed, mating (Julian date 145–220), hyperphagia (Julian date 213–273) and hunting (Julian date 233–288) seasons. The green dotted vertical (break estimate) and green solid lines (5% and 95% confidence intervals) correspond to the breaks defined by the uninformed model. The identified breaks by the null model and their corresponding day of the year can be found in the small table. Here, the break (left, middle, right), break estimate and 5%–95% confidence interval (CI) values for the estimate are given. The shaded area is the period with the highest frequency of female–male associations.

**Table 1**
For all candidate models, the calculated AICc value and the delta AICc as the difference between the SBA models using female–male association based on GPS data from brown bears in south-central Sweden (2003–2022)

| Model | Hypothesis | AICc | ΔAICc |
|---|---|---|---|
| **Uninformed** | **Identify seasons** | **2030** | — |
| Mating | Reproduction (1) | 2336 | 306 |
| Mating+Hyperphagia | 1+2 | 2338 | 308 |
| Mating+Hunting | 1+3 | 2338 | 308 |
| Mating+Hyperphagia+Hunting | 1+2+3 | 2340 | 310 |
| Hyperphagia | Food resources (2) | 2471 | 441 |
| Hunting | Avoidance/Refuge (3) | 2472 | 442 |
| Hyperphagia+Hunting | 2+3 | 2473 | 443 |

The most parsimonious model is highlighted in bold.

candidate models included the mating season variable (Table 1). The models with additional variables (hyperphagia or hunting) are within the set ΔAICc threshold, but these are likely uninformative parameters (Arnold, 2010). Similar patterns were found using all associations and uniformly for all three classes (F-M, M-M, F-F; Fig. 2, Figs A3–A5).

*Annual and Seasonal Social Networks*

We analysed annual and seasonal networks based on GPS data using the three distance thresholds (i.e. 100, 200 and 500 m). As the candidate model with mating seasons best explained the association frequency for males and females, we used the analysis regarding the female–male associations as the classification between seasons for the SNA (Fig. 2). The results suggest that the mating season lasts from Julian date 135 (15 May) to 202 (21 July), with the highest frequency occurring between Julian date 145 (25 May) and 151 (31 May).

Associations occur nonrandomly in frequency and number of unique dyads during the active period (example 2008: Fig. 3), and the same patterns are visible when applying a dynamic approach

by using the mating and non-mating season. Similar patterns are found when using either of the three distance thresholds (Fig. 3, Figs A6–A8). For both the ratio of observed versus available unique dyads (density) and the average association index per individual (mean strength), the observed network metric values were generally outside the distribution range of the random networks. For 2012, using all distance thresholds, the observed network values and random distributions overlapped for either the density, strength or both metrics; this is likely caused by a low spatiotemporal overlap of GPS-collared individuals in the population that year and thus a low robustness of the network (Fig. A9). Generally, the metrics show that the observed social networks are more connected then random (i.e. more unique dyads) with higher frequency and longer duration of associations per unique dyad, and consequently mean strength is the main contrast between the observed and random networks.

**DISCUSSION**

Our results showed seasonally distinctive frequencies in brown bear associations throughout their active period. We found support for prediction (1), that reproduction is the main driver for associations in the population, that is, the highest frequency of associations occurring during the mating season and male–female associations during the mating season included the majority (73%) of observed brown bear dyads. We also observed dyad associations during the hyperphagia and hunting seasons; however, there was limited support for our predictions (2) and (3), as we did not find changes in frequency during these seasons. Our prediction (4) was only partially supported, that is, we found that social structures during the mating season were nonrandom, but contrary to our prediction, we found that associations also occurred more often than expected during the nonmating season. This suggests that bears intentionally associate with conspecifics during both seasons.
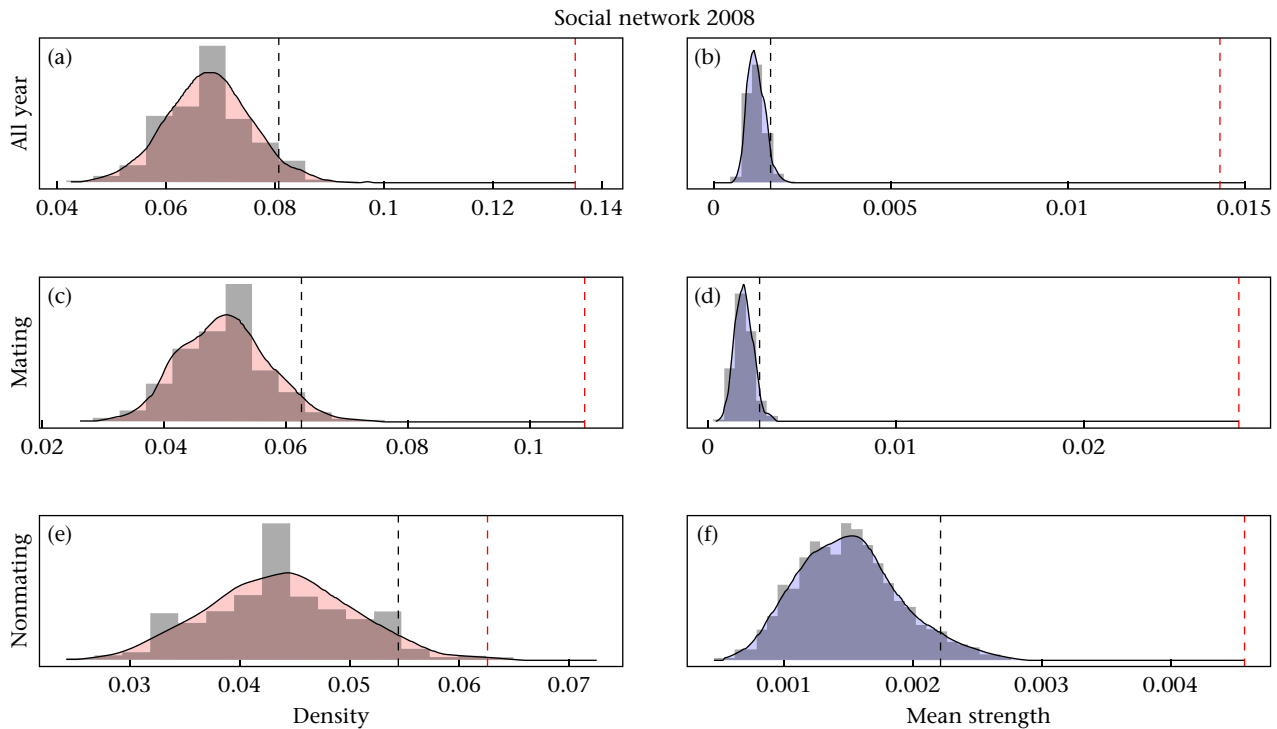
Social network 2008



**Figure 3.** Random distributions (999 iterations) versus observed network metric values (density and mean strength) based on data (200 m associations) from the brown bear population in south-central Sweden in 2008. The random network distributions per metric (shaded area) are shown (a-b) on an annual basis and (c-f) per season (c-d: mating; e-f: nonmating). The grey bars represent the histogram of the 999 random network metrics. Per period and network metric, the observed network metric value is indicated by the red dashed line and the black dashed line is the 95% confidence interval from the random network metric distributions.

The first step of the SBA, using female–male associations (Fig. 2), shows a clear delineation of the mating season lasting from early May to mid-July (Spady et al., 2007), suggesting that the mating season of brown bears is likely shorter than previously determined. Moreover, we identified two subperiods during the mating season, with a main peak in associations between mid-May and mid-June and a second, smaller, one, from mid-June to mid-July. Although, we do not have behavioural observations of mating events, we hypothesize that the second peak may be related to a second oestrus cycle (Craighead et al., 1995; Spady et al., 2007). This second peak could also represent two other scenarios: (1) males might focus on 'available' solitary females first and only later initiate associations with females with cub(s) which could lead to sexually selected infanticide (SSI) and therefore the peak is initiated due to a delayed oestrus; or (2) the receptive females that did not mate with any males during the first peak do so in the second oestrus cycle. However, these scenarios remain to be tested. Previous studies on this population showed that 95% of the cub mortality occurs during the mating season and for all cubs that were recovered during that period the cause of death was SSI (Gosselin et al., 2015). To prevent future SSI events, females increase their promiscuity even when they are already fertilized by other males (Bellemain et al., 2006). Increased promiscuity by females also increases male–male competition, sperm competition and the production of high-quality offspring (Simmons, 2005). Therefore, this strategy may enhance opposite-sex sociality and promote more social individuals, showcasing the relationship between reproductive strategies and social flexibility (Kappeler et al., 2013; Quaglietta et al., 2014; Schradin, 2013).

In general, reproduction is the main motivation for associations between conspecifics as it is directly linked to individual fitness (Fisher & McAdam, 2017; Silk, 2007). For example, more opposite-sex associations between house sparrows, *Passer domesticus*, increased an individual's annual fitness (Dunning et al., 2023). For brown bears, we found that reproduction is also the main factor structuring their sociality. We further found that brown bears (both female–male and same sex) associate more often than expected by chance outside the mating season (i.e. during hyperphagia and hunting seasons); however, the benefit of these associations is not clearly understood. Here, we highlight three plausible explanations (i.e. food, humans, carryover effect) for why solitary species could be motivated to associate outside the mating season. First, food resources have been identified as an attractant that causes brown bears to aggregate and tolerate conspecifics (Stonorov & Stokes, 1972; Wirsing et al., 2018). Also, in other solitary species (e.g. puma, *Puma concolor*, raccoon, *Procyon lotor*, and vultures, *Gyps* spp.), local food availability affected an individual's social behaviour (Deygout et al., 2010; Elbroch et al., 2017; Wehtje & Gompper, 2011). In our study population in Scandinavia, the food resources (ants, *Formica* spp., *Camponotus* spp., moose, *Alces alces*, berries, *Vaccinium* spp.) are relatively uniformly distributed across the landscape (Dahle et al., 2013; Frank et al., 2015; Stenset et al., 2016), in contrast to other brown bear populations (Proctor et al., 2023; Wirsing et al., 2018), and therefore an unlikely motivation for associations. In Scandinavia, brown bears primarily prey on neonate moose calves between May and June and rarely kill adult moose (Dahle et al., 2013; Swenson et al., 2007; Tallian et al., 2017). Moose carcasses are an unlikely source for associations of bears in Scandinavia, as neonate calves are consumed quickly and almost no remains are left (Ordiz et al., 2020). Yet, the presence of wolves and local hunting practices (e.g. bait sites and slaughter remains from hunting; Brown et al., 2023) may provide access to additional carcasses, and it is possible that we underestimated food-based associations because of the coarse GPS fix rate of 1 h (i.e. GPS collars on all individuals only take one GPS location per h; Bischof et al., 2008; Tallian et al., 2017). Second, human activities such as

hunting affect animal movement (Tucker et al., 2018) and social structures (Williams & Lusseau, 2006). In our population, harvest has led to extensive behavioural adaptations in terms of movement, reproduction and social structures (Brown et al., 2023; Frank et al., 2017; Gosselin et al., 2017; Van De Walle et al., 2018). For example, the spatial configuration of bears is affected by harvest, with age, sex and relatedness as the strongest factors influencing the use of hunter-created vacancies by survivors (Frank et al., 2018). Additionally, in Sweden, hunting regulations prohibit hunters from harvesting females accompanied by offspring, which has caused females to increase the duration of maternal care which likely affects their sociality (Van de Walle et al., 2019, 2021). This shows how harvest leads to unnatural social structures and adaptations in life history. Although, we did not find a distinctive change in the frequency of associations during the hunting season, it is likely affecting the future sociality of individuals by increasing the chance of SSI or unstable dominance hierarchies (Leclerc et al., 2017; Zedrosser et al., 2007). Lastly, the social competence of individuals ensures they benefit from available social information and consequently build relationships (Silk & Hodgson, 2021; Taborsky & Oliveira, 2012). This information can be carried over between seasons, influencing future mating events and same-sex associations (Firth & Sheldon, 2016; Kurvers et al., 2020). Therefore, brown bear associations during the nonmating season could be related to reproduction as well as dominance hierarchies (Hansen et al., 2023; Zedrosser et al., 2007), for example, by individuals searching out mating partners of the previous mating season and by taking stock of competitors or potential mates for the next mating season. These associations might be less frequent and of shorter duration than in the mating season, but additional nonphysical or indirect associations (e.g. scent-scape) might offer conclusive information regarding the reproductive status of neighbouring conspecifics (Morehouse et al., 2021; Revilla et al., 2021). Thus, linking spatial (e.g. resource patches) and social (e.g. dyads that interacted the previous season) variables might give more insight into why and with whom individuals interact outside the mating season and potentially associated fitness benefits.

Animal sociality is commonly viewed as a classification of social versus nonsocial (Blonder et al., 2012; Farine, 2018), but our results suggest that it is rather a dynamic continuum (Webber & Vander Wal, 2018) primarily influenced by variations in a species' spatio-temporal configuration (i.e. seasonal movements, social unit structure) and demographic composition (i.e. age, sex). Our results also support the contention that animal sociality investigations should include a sociospatial perspective, as both components are tightly linked (Webber et al., 2023; Webber & Vander Wal, 2019). The sociospatial environment of a population is under constant change, as variations in factors such as seasonality (e.g. summer/winter), availability of resources (e.g. food, mates), diel activity patterns (e.g. dusk/dawn), human activities (Williams & Lusseau, 2006) or kinship can result in behavioural changes (Graw et al., 2019; Robert et al., 2013; Silk et al., 2017). Additionally, brown bears are one of many species (Doherty et al., 2021; Lewis et al., 2021) whose population dynamics are also heavily affected by humans (Frank et al., 2017; Gosselin et al., 2015), and disrupting social structures within a population might strengthen this effect over time (Frank et al., 2021; Gosselin et al., 2017). As sociality can affect individual fitness (Formica et al., 2012; Silk et al., 2010), and vice versa, advancing knowledge of 'solitary' species is paramount for the conservation and sustainable management of their populations (Olivier et al., 2022; Vander Wal et al., 2012; Wey et al., 2013). Further studies should, therefore, focus on investigating the mechanisms and attributed fitness benefits promoting associations outside a mating season, the occurrence of reproductive strategies in relation to sociality, and the immediate and long-term effects of hunting practices on animal sociality.

## Author Contributions

**Rick W. Heeres:** Writing – review & editing, Writing – original draft, Methodology, Formal analysis, Data curation, Conceptualization. **Martin Leclerc:** Writing – review & editing, Methodology, Conceptualization. **Shane Frank:** Writing – review & editing, Methodology, Conceptualization. **Alexander Kopatz:** Writing – review & editing, Project administration. **Fanie Pelletier:** Writing – review & editing, Supervision, Conceptualization. **Andreas Zedrosser:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization.

## Data Availability

The data that support the findings of this study are available on our universities' USN Research Data Archive (https://doi.org/10.23642/usn.24949185.v1).

## Declaration of Interest

The authors declare no conflict of interest.

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## Appendix

**Table A1**
For all candidate models, the calculated AICc value, and the delta AICc as the difference between models using all associations during the year by all sex groups (female–male, male–male, female–female) based on GPS data from brown bears in south-central Sweden (2003–2022)

| Model | Hypothesis | AICc | ΔAICc |
|---|---|---|---|
| **Uninformed** | **Identify seasons** | **2141** | — |
| Mating | Reproduction (1) | 2416 | 275 |
| Mating+Hyperphagia | 1+2 | 2417 | 276 |
| Mating+Hunting | 1+3 | 2417 | 276 |
| Mating+Hyperphagia+Hunting | 1+2+3 | 2419 | 278 |
| Hyperphagia | Food resources (2) | 2561 | 420 |
| Hunting | Avoidance/Refuge (3) | 2562 | 421 |
| Hyperphagia+Hunting | 2+3 | 2563 | 422 |

The most parsimonious model is highlighted in bold.

**Table A2**
For all candidate models, the calculated AICc value, and the delta AICc as the difference between the SBA models using female–female associations based on GPS data from brown bears in south-central Sweden (2003–2022)

| Model | Hypothesis | AICc | ΔAICc |
|---|---|---|---|
| **Uninformed** | **Identify seasons** | **1649** | - |
| Mating+Hyperphagia | 1+2 | 1811 | 162 |
| Mating+Hyperphagia+Hunting | 1+2+3 | 1813 | 164 |
| Mating | Reproduction (1) | 1815 | 166 |
| Mating+Hunting | 1+3 | 1815 | 166 |
| Hyperphagia | Food resources (2) | 1921 | 272 |
| Hunting | Avoidance/Refuge (3) | 1924 | 275 |
| Hyperphagia+Hunting | 2+3 | 1923 | 274 |

The most parsimonious model is highlighted in bold.

**Table A3**
For all candidate models, the calculated AICc value, and the delta AICc as the difference between the SBA models using male–male associations based on GPS data from brown bears in south-central Sweden (2003–2022)

| Model | Hypothesis | AICc | ΔAICc |
|---|---|---|---|
| **Uninformed** | **Identify seasons** | **1213** | — |
| Mating+Hyperphagia | 1+2 | 1224 | 12 |
| Mating+Hunting | 1+3 | 1225 | 13 |
| Mating+Hyperphagia+Hunting | 1+2+3 | 1226 | 14 |
| Mating | Reproduction (1) | 1227 | 15 |
| Hyperphagia | Food resources (2) | 1271 | 59 |
| Hunting | Avoidance/Refuge (3) | 1272 | 60 |
| Hyperphagia+Hunting | 2+3 | 1273 | 61 |

The most parsimonious model is highlighted in bold.
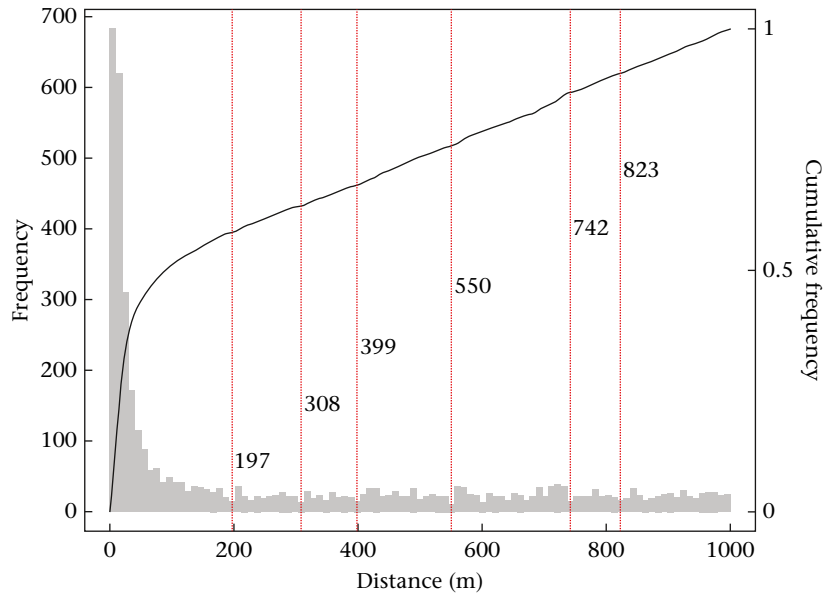
**Figure A1.** Natural breaks analysis on the dyad frequency and the distance between individuals (of either sex) based on GPS data from the brown bear population in south-central Sweden (2003–2022). The 'wildlifeDI' package (Long et al., 2022) was used to create the figure.
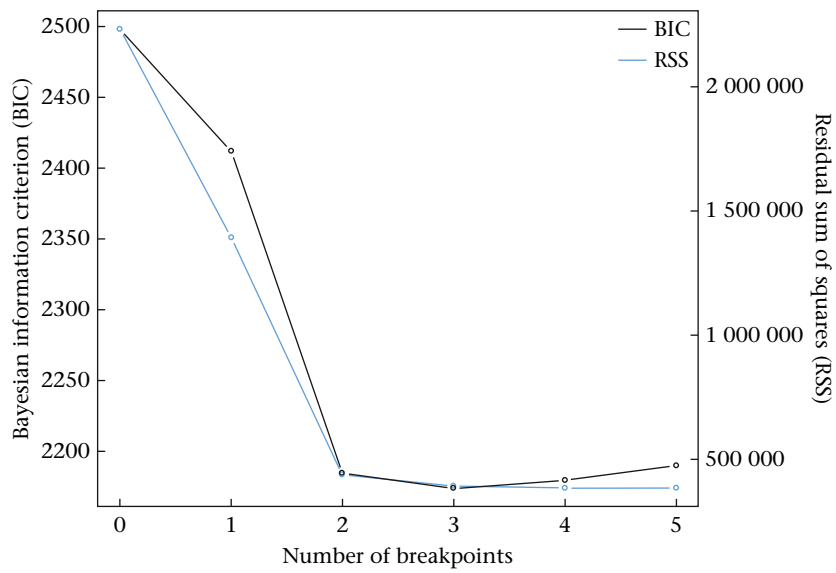


**Figure A2.** Model selection for the null hypothesis structural break model based on the Bayesian information criterion using the frequency of association calculated by using the GPS data from the brown bear population in south-central Sweden (2003–2022).
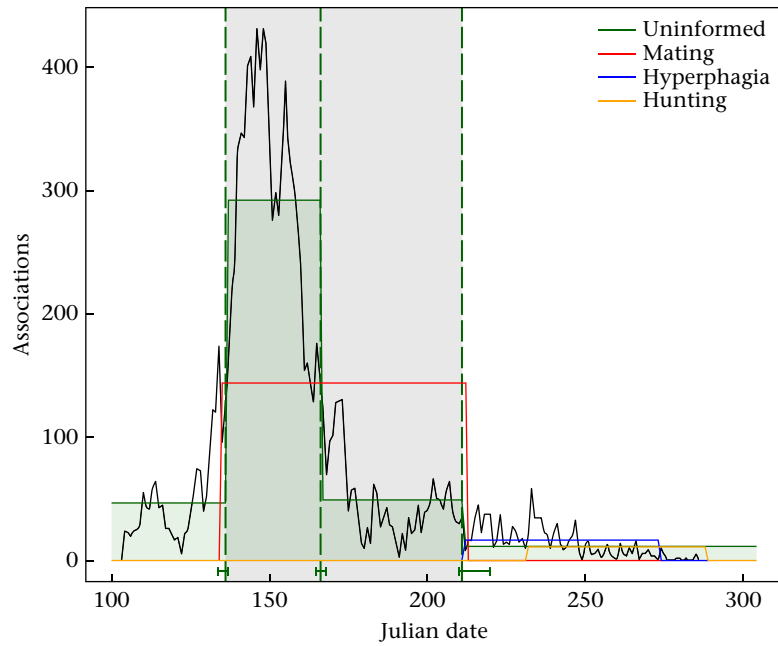
**Figure A3.** Time series plot showing the frequency of associations (black solid line) during the year (Julian date) by all sex groups (female–male, male–male, female–female) based on GPS data from brown bears in south-central Sweden (2003–2022). The lines are the output of the SBA models regarding the uninformed, mating (Julian date 145–220), hyperphagia (Julian date 213–273) and hunting (Julian date 233-288) seasons. The green dotted vertical (break estimate) and green solid lines (5% and 95% confidence intervals) correspond to the breaks defined by the uninformed model. The shaded area is the period with the highest frequency of female–male associations.
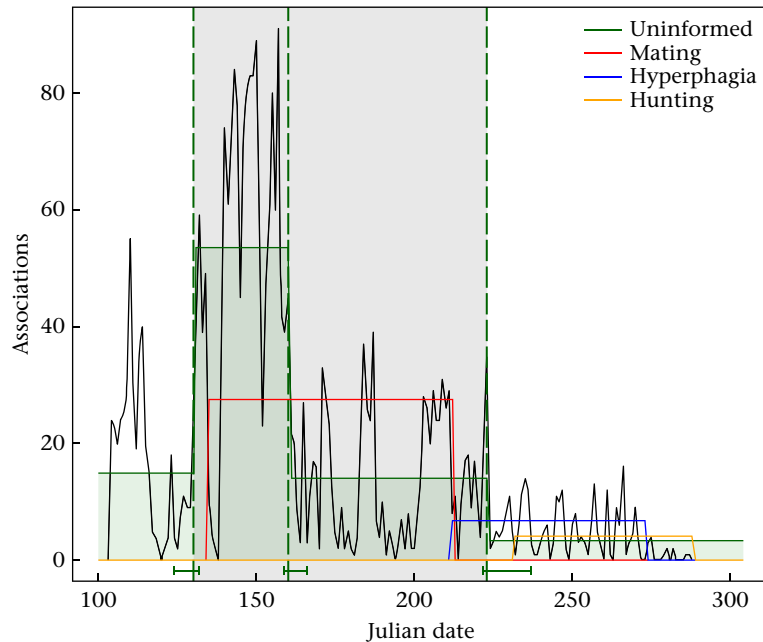


**Figure A4.** Time series plot showing the frequency of associations during the year (Julian date) by female–female dyads based on GPS data from brown bears in south-central Sweden (2003–2022). The lines are the output of the SBA models regarding the uninformed), mating (Julian date 145–220), hyperphagia (Julian date 213–273) and hunting (Julian date 233–288) seasons. The green dotted vertical (break estimate) and green solid lines (5% and 95% confidence intervals) correspond to the breaks defined by the uninformed model. The shaded area is the period with the highest frequency of female-male associations.
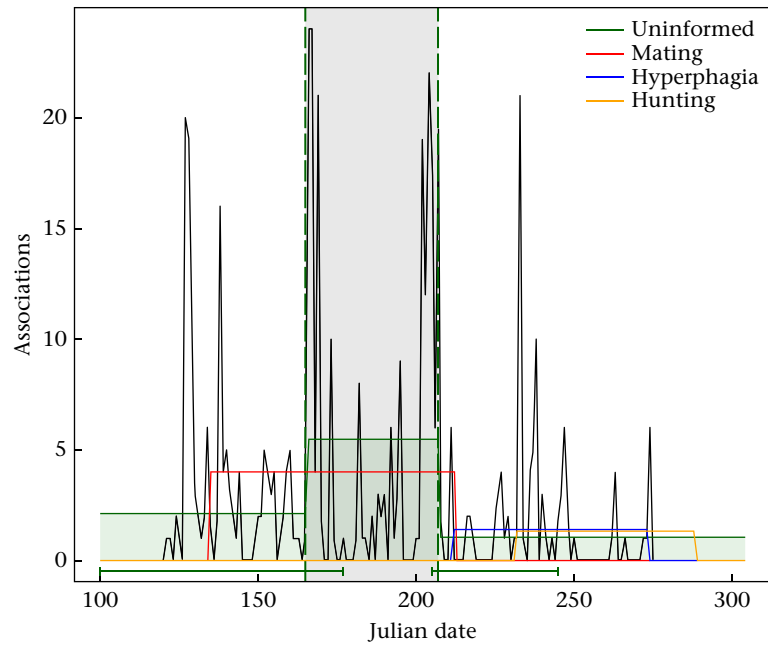
**Figure A5.** Time series plot showing the frequency of associations during the year (Julian date) by male–male dyads based on GPS data from brown bears in south-central Sweden (2003–2022). The lines are the output of the SBA models regarding the uninformed, mating (Julian date 145–220), hyperphagia (Julian date 213–273) and hunting (Julian date 233–288) seasons. The green dotted vertical (break estimate) and green solid lines (5% and 95% confidence intervals) correspond to the breaks defined by the uninformed model. The shaded area is the period with the highest frequency of female-male associations.
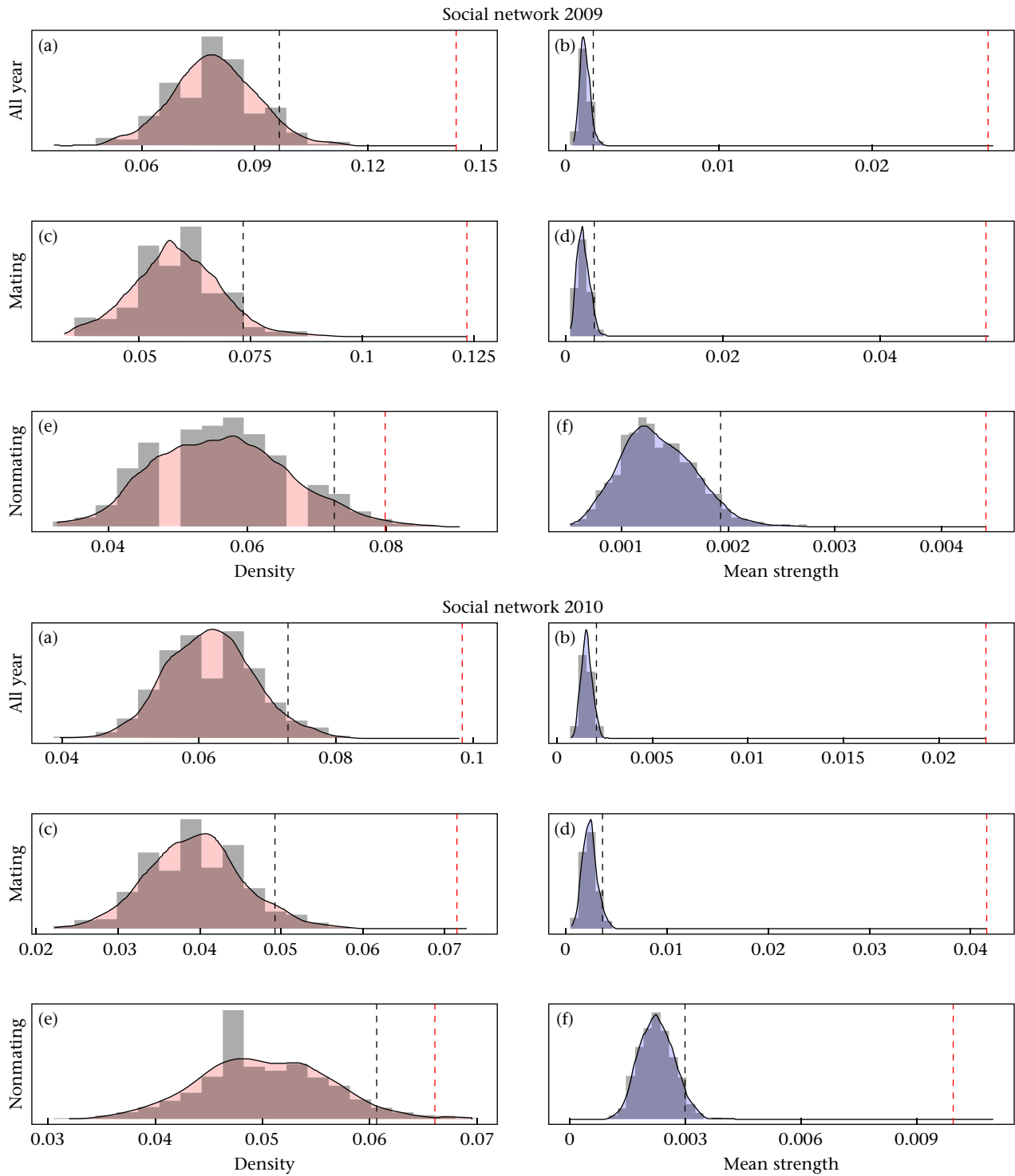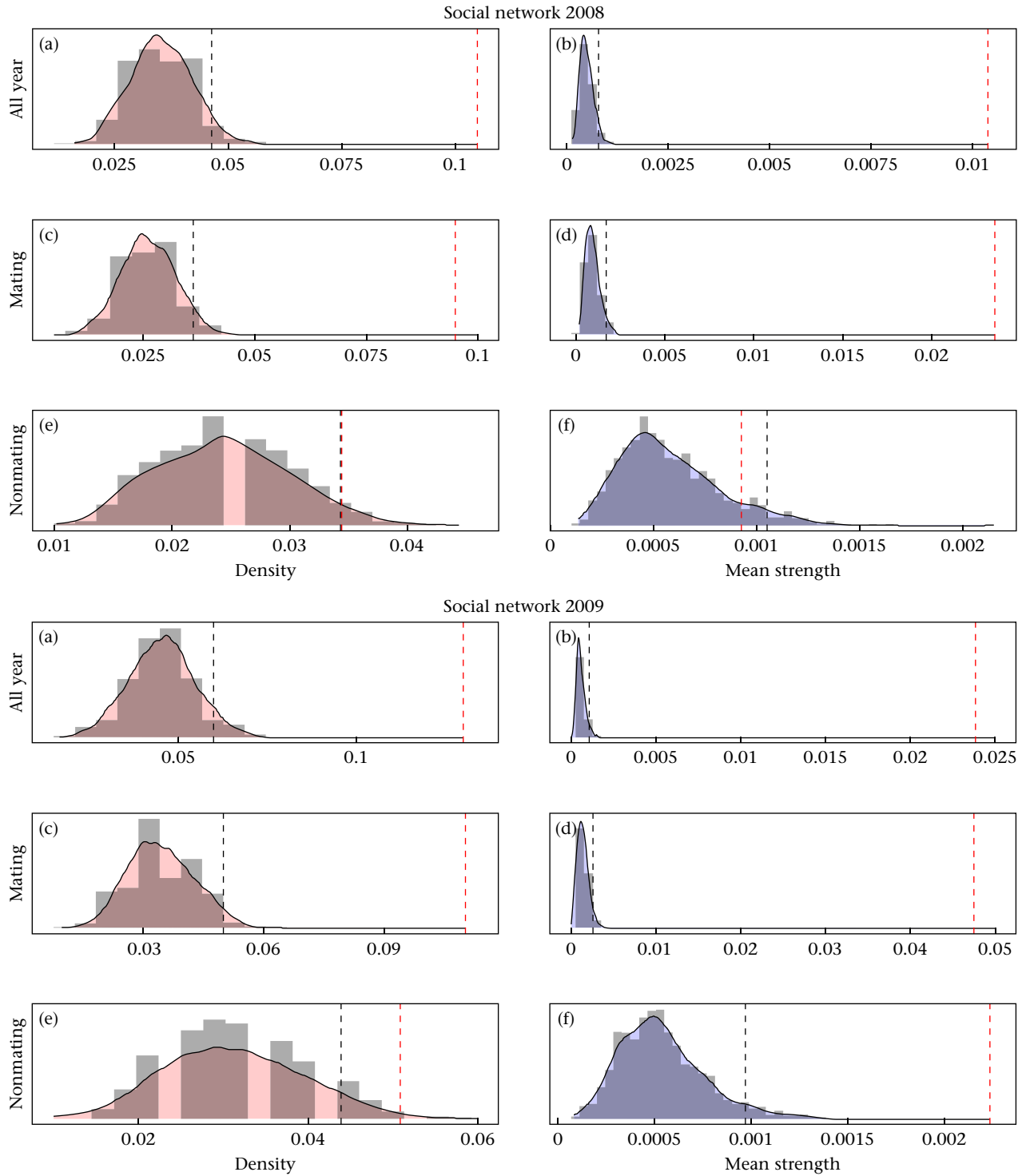
**Figure A6.** Random (999 iterations) distributions versus observed network metric values (density and mean strength) based on data from the brown bear population in south-central Sweden in 2009–2014 (200 m distance threshold). The random network distributions per metric (shaded area) are shown (a-b) on an annual basis and (c–f) per season (c–d: mating; e–f: nonmating). The grey bars represent the histogram of the 999 random network metrics. Per period and network metric, the observed network metric value is indicated by the red dashed line and the black dashed line is the 95% confidence interval from the random network metric distributions.
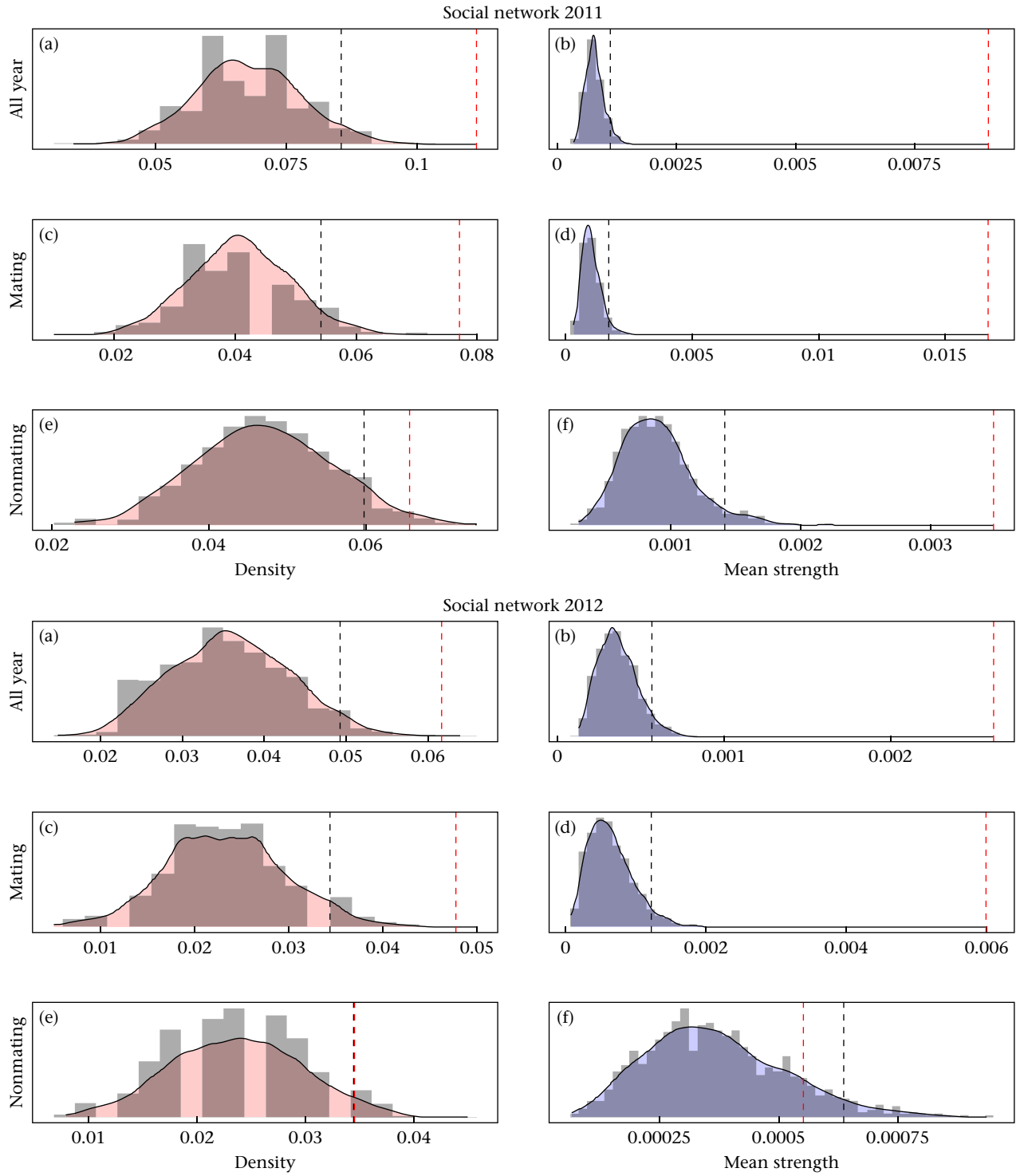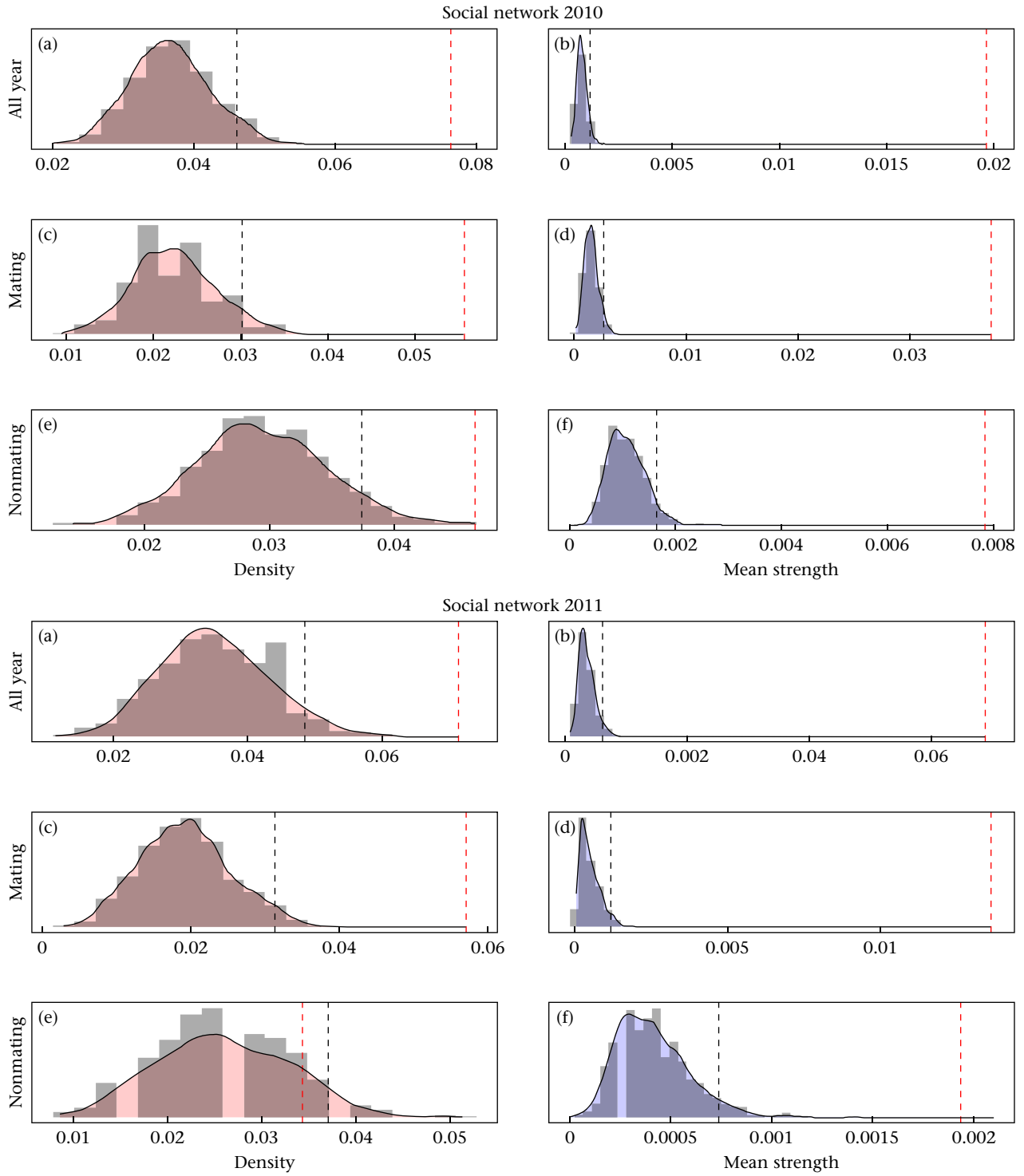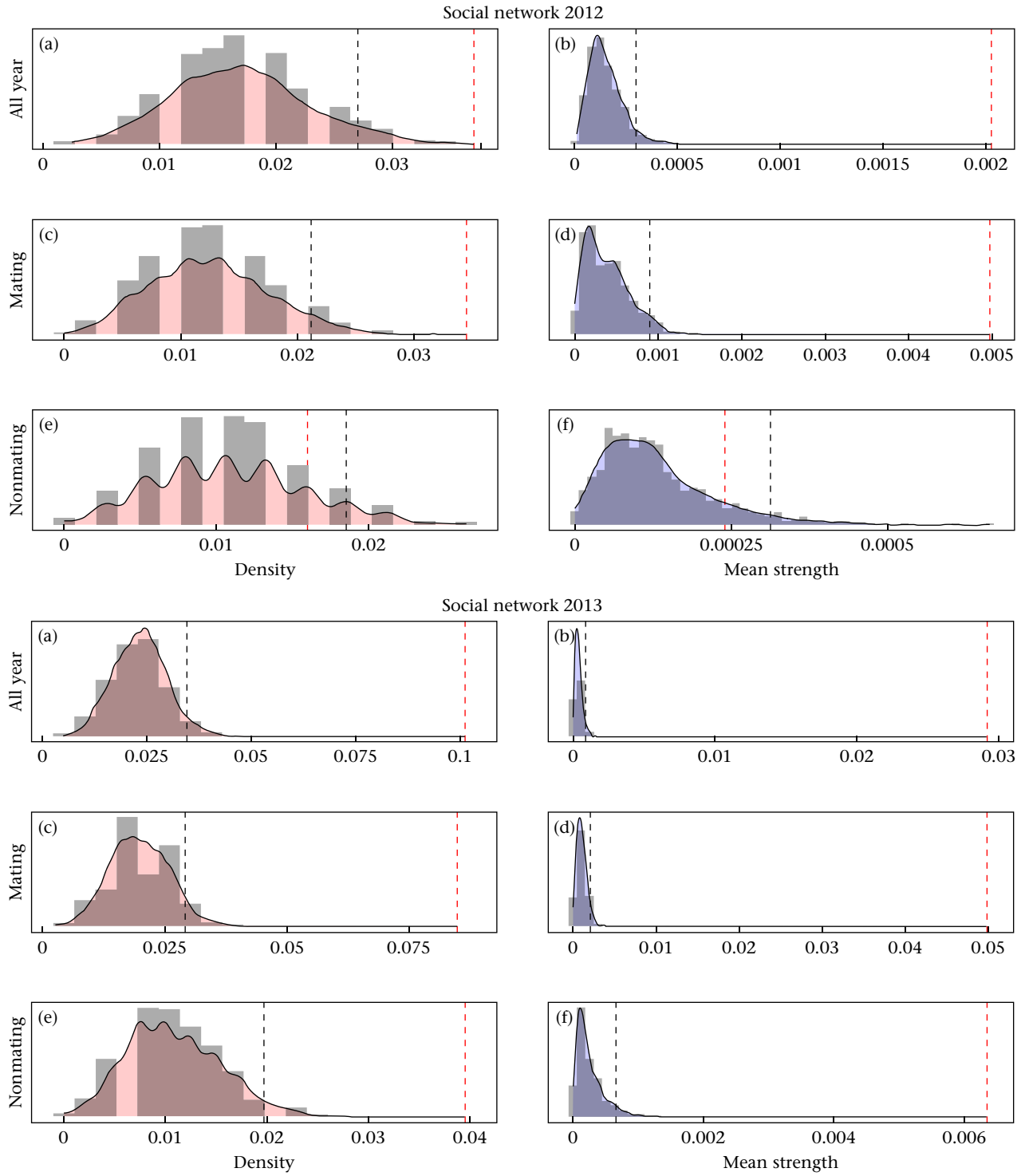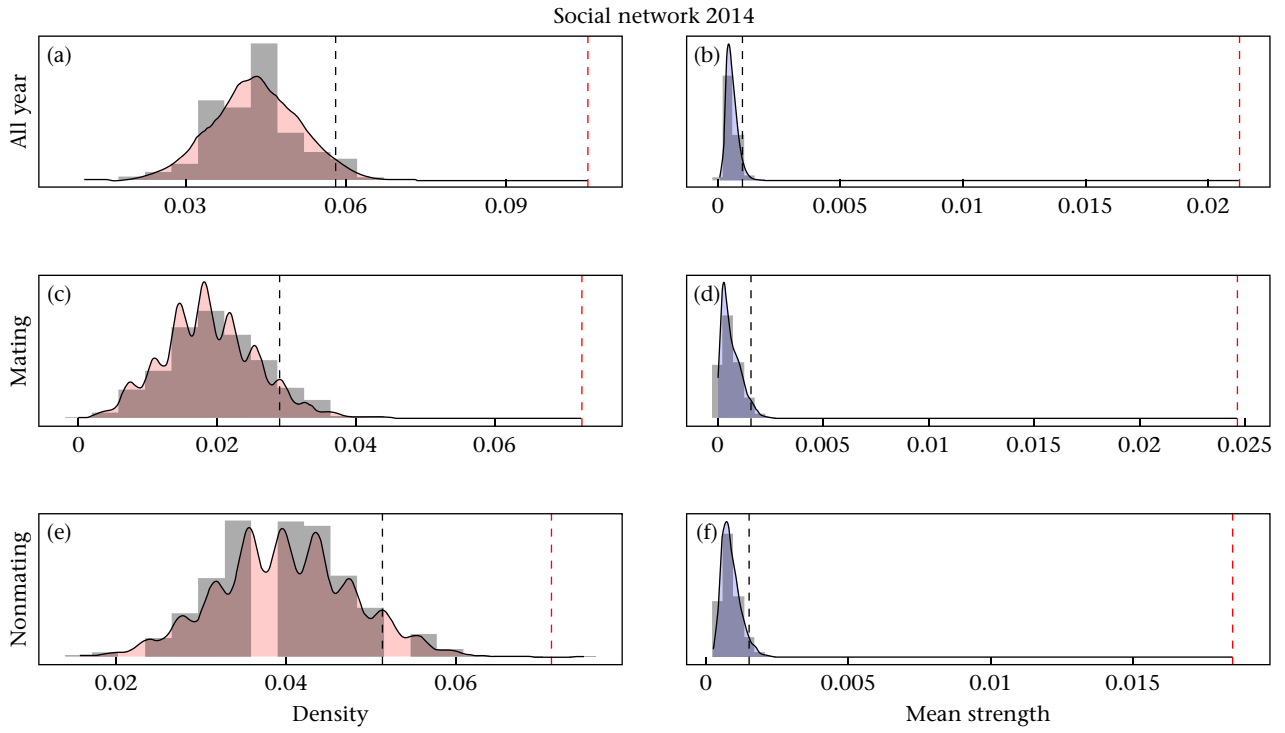
**Figure A6.** (*continued*).
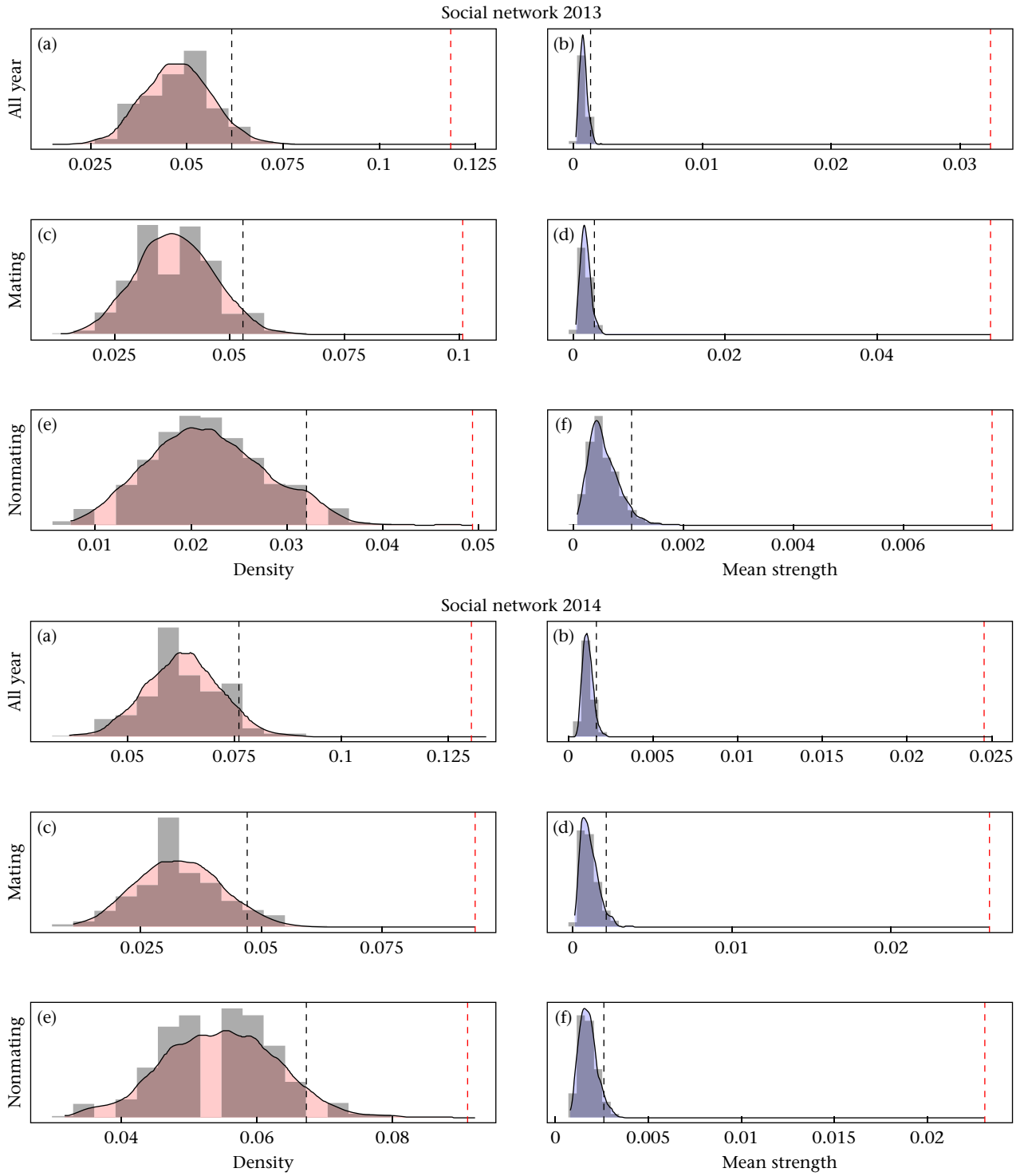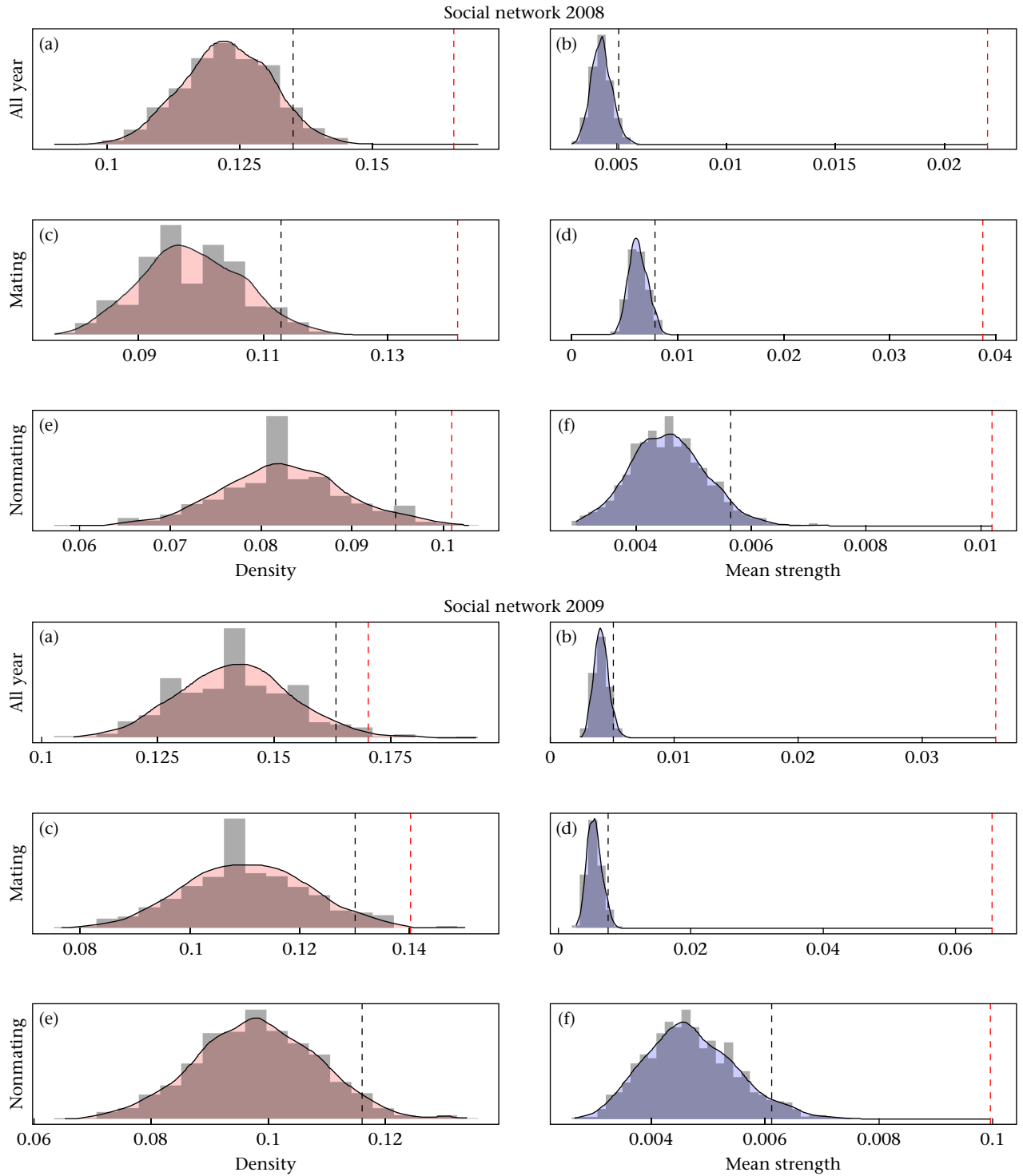
**Figure A6.** (*continued*).

**Figure A7.** Random (999 iterations) distributions versus observed network metric values (density and mean strength) based on data from the brown bear population in south-central Sweden in 2008–2014 (100 m distance threshold). The random network distributions per metric (shaded area) are shown (a–b) on an annual basis and (c–f) per season (c–d: mating; e-f: nonmating). The grey bars represent the histogram of the 999 random network metrics. Per period and network metric, the observed network metric value is indicated by the red dashed line and the black dashed line is the 95% confidence interval from the random network metric distributions.
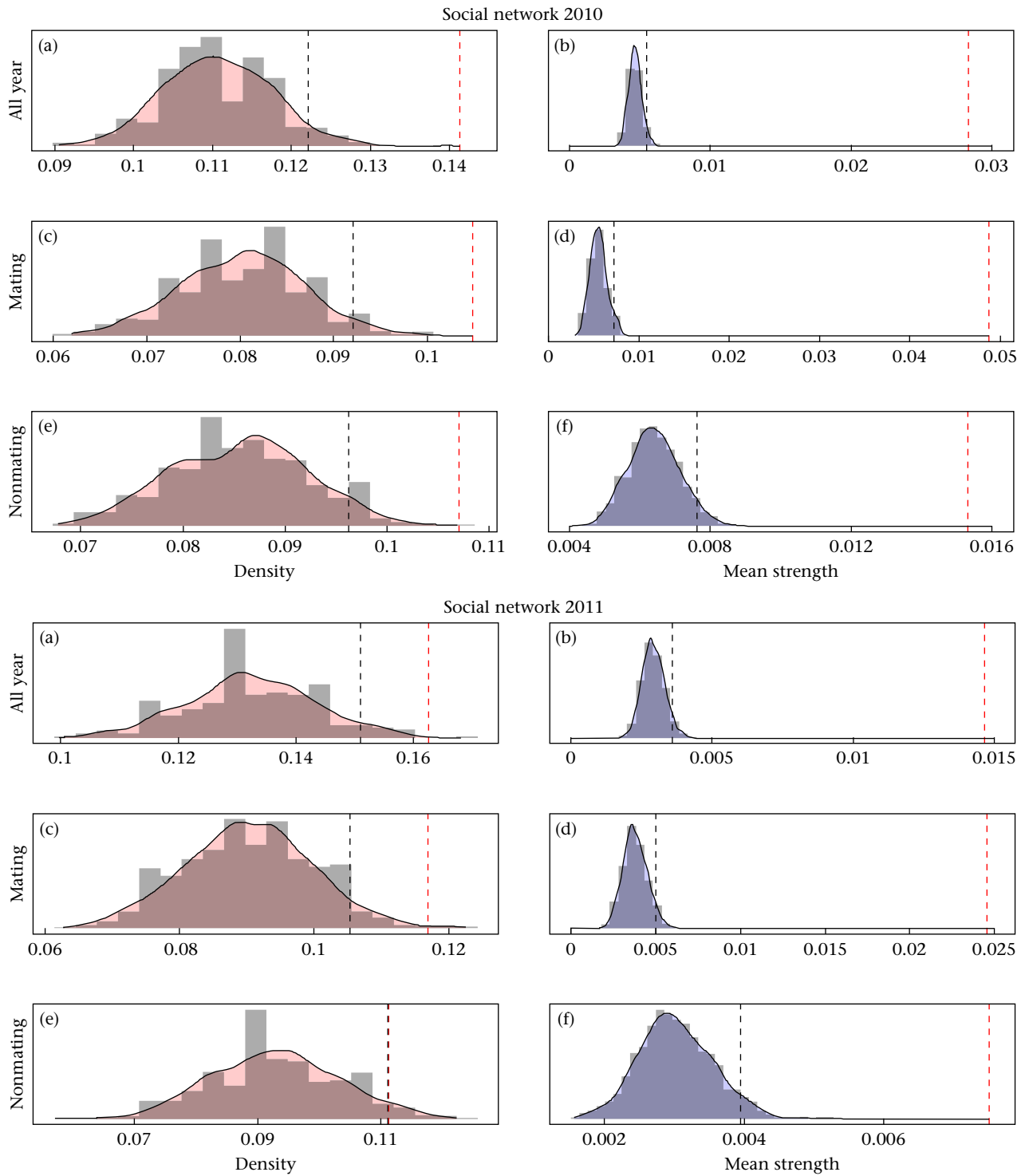
**Figure A7.** (*continued*).

Social network 2012



Social network 2013



**Figure A7.** (*continued*).

**Figure A7.** (*continued*).

**Figure A8.** Random (999 iterations) distributions versus observed network metric values (density and mean strength) based on data from the brown bear population in south-central Sweden in 2008—2014 (500 m distance threshold). The random network distributions per metric (shaded area) are shown (a—b) on an annual basis and (c—f) per season (c—d: mating; e—f: nonmating). The grey bars represent the histogram of the 999 random network metrics. Per period and network metric, the observed network metric value is indicated by the red dashed line and the black dashed line is the 95% confidence interval from the random network metric distributions.
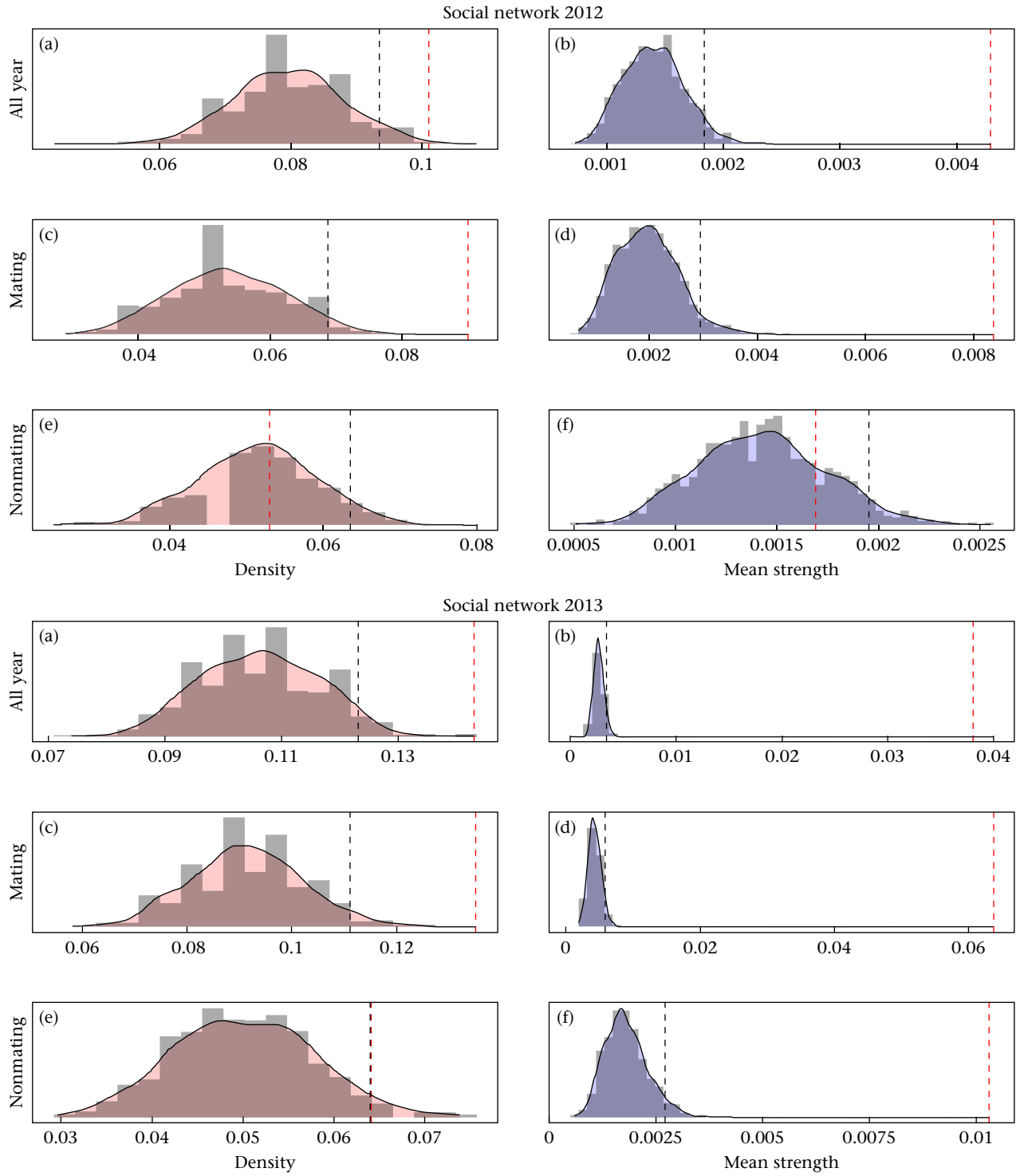
**Figure A8.** (*continued*).

**Figure A8.** (*continued*).
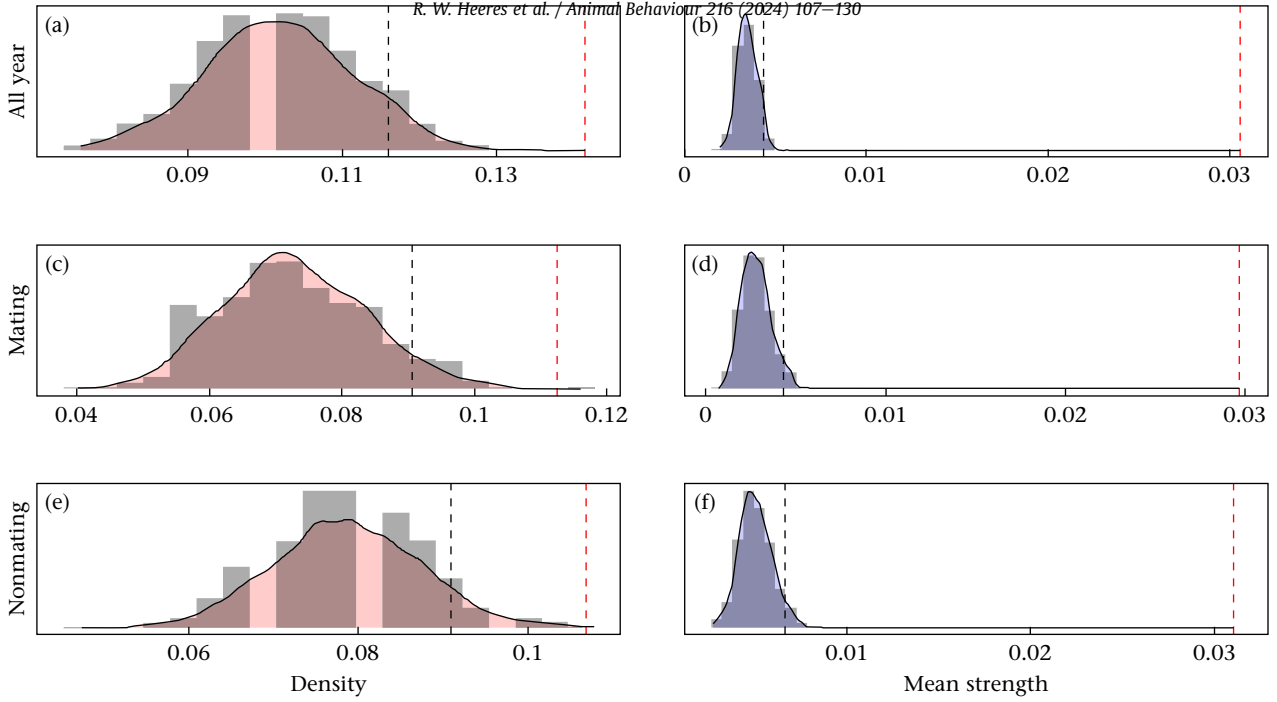
Social network 2014



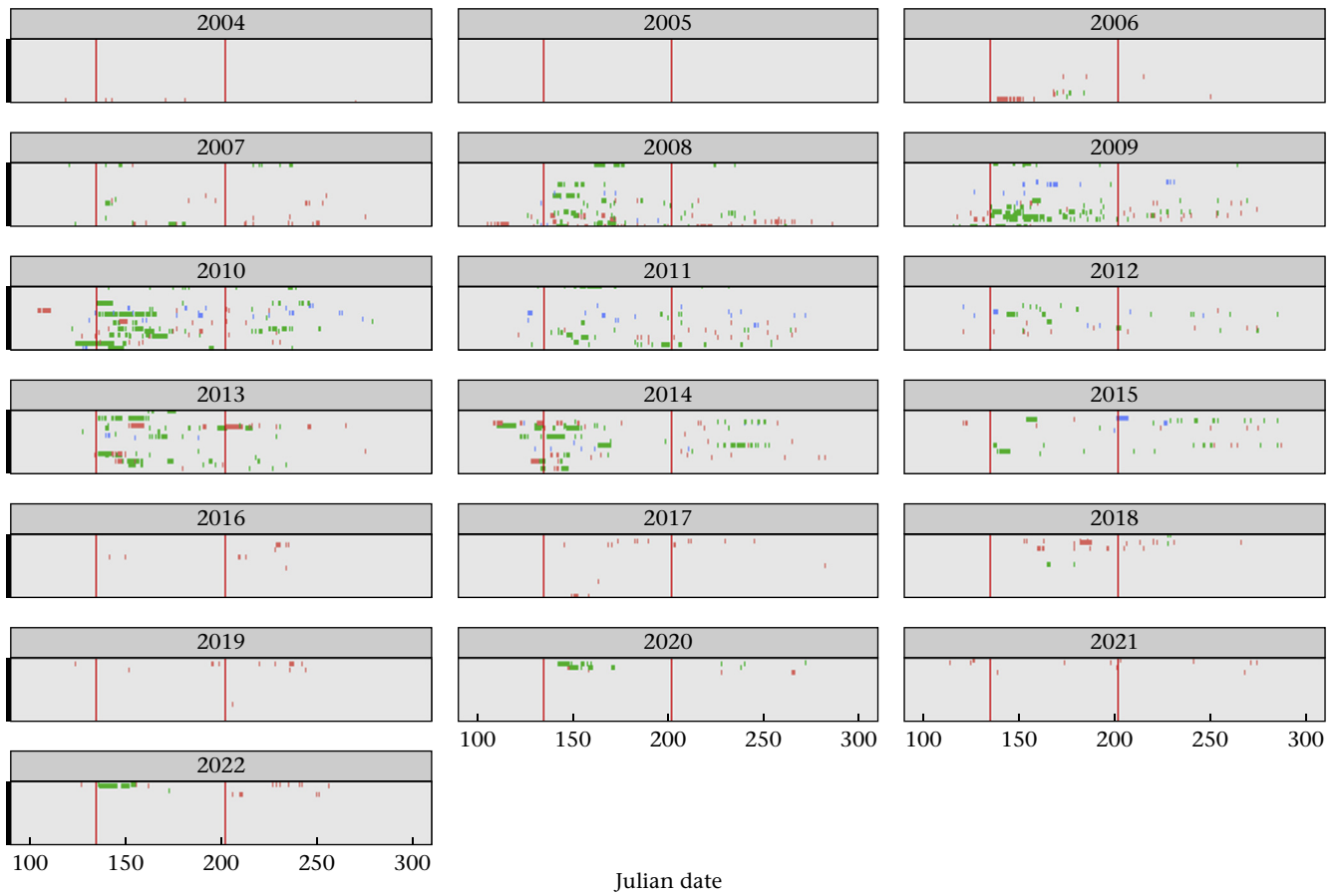**Figure A8.** (*continued*).



**Figure A9.** The overview of associations per individual over time (Julian date) divided per year. Classified and coloured by sexes participating in the association: F–F = red, F–M = green and M–M = blue. The red vertical lines indicate the mating season based on the natural break analysis.