Detection probabilities and absolute densities of birds in trees

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For a study of long-distance migrants in sub-Saharan Africa, a census method was developed that combined precision and accuracy regarding bird numbers and tree choice. The number of birds present in trees and shrubs can be counted accurately, although it is time-consuming. We describe how much time is needed to detect all birds present in trees, using data collected in over 2000 plots across West Africa during the dry season (October–March in 2007–2015). The observation time per tree depended on tree size, number of birds present and the opacity of the crown. The giving-up time of the observers increased with canopy volume, but was independent of the number of birds in a tree. Detection probabilities of bird species differed relative to microhabitat choice and feeding techniques. Species-specific detectabilities hardly varied during the day or the season. All foraging birds and immobile birds (save a few percent in dense canopies) were detected using the individual-tree-approach. Bird density is expressed as number per canopy volume, but little information is lost when density is given as number per canopy surface. The variation in bird density was large and differed per tree species. Within tree species, bird density was related to the opacity of the crown, the abundance of insects and whether there were berries or flowers. These findings suggest that, to collect biologically relevant information, the density of tree-dwelling birds should be measured at the level of the individual tree, and not per surface area, habitat type or tree species (as is typical in published studies).

Key words: insectivorous birds, bird density in trees, detection probability, tree canopy, Sahel

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Ever since counting birds became more than a hobby, attempts have been made to come to grips with the problems that surface when reliable (i.e. closely resembling reality) and reproducible data on bird numbers are to be obtained (Bibby *et al.* 1992). Standardization of census methods has come a long way, but most methods still produce only an index value of abundance. No matter how many procedures are followed to upgrade the quality of the census, indices are poor value if detection probability varies through space and time and between species (Anderson 2003). This problem is aggravated when no attempts are made to obtain valid estimates of precision, notably estimates of detection probabilities (reviewed by Bächler & Liechti 2007).

Even when the detection probability is quantified and absolute bird numbers are known and validated,

the question remains how to convert numbers into density and a reliable description of habitat choice. In our study of the fortunes of Palearctic tree-dwelling birds wintering in sub-Saharan Africa, for example, it was clear from the start that a description of habitat choice and density should hinge on detailed observations of the birds' tree choice (Zwarts *et al.* 2015, see also Peck 1989, Gabbe *et al.* 2002, Wood *et al.* 2012). Absolute bird density at the tree level was a priority to adequately describe how birds use their wintering habitats and to explain how changes in numbers may have materialised (see also Fuller 2012, for many well-argued pleas in favour of in-depth studies of habitat choice).

Hence, we disregarded the use of bird densities per surface area or per habitat type and instead focused our attention on the birds' use of individual trees, to

account for the temporal and spatial variation in tree choice and tree properties. Taking this step sent us stumbling into other methodological pits. For example, the density of tree-dwelling birds can be expressed per canopy surface or per canopy volume. If bird densities could be accurately expressed as numbers per canopy surface (i.e. in two dimensions), we might in further analyses use aerial photographs and high resolution satellite images to estimate bird numbers through measuring canopy surface over vast areas of land. But how to obtain reliable data on canopies, and which measure is the most biologically meaningful when comparisons are made of bird densities in different tree species (Spurr & Warburton 1991) or in trees with different canopy height (Goetz *et al.* 2007)? And finally, how to anticipate a woody vegetation that consists of a heterogeneous assemblage of different trees and shrubs. Valuable information is lost when birds and tree species are summed per site, even when converted into bird densities per tree species. To avoid such generalisations, bird numbers had to be collected separately for each individual tree and shrub, at the same time obtaining data on tree dimensions, density of foliage, and fruiting and flowering conditions. It would be difficult, and sometimes even impossible, to collect these data per tree in continuous woodland, but quite feasible in open landscapes with scattered trees where canopies do not touch or overlap. The next step, beyond the scope of this paper, is to analyse whether distance between trees, tree density and the distribution of different tree species have an additional impact on bird densities.

We feel that Sahelian-wide generalisations about bird numbers and changes therein over time are only possible when using absolute densities, even when this entails a time-consuming method to study bird-habitat relationships. If we know the bird density per ha canopy for the different tree species as well as the total woody cover of these tree species across the wintering area, several generalisations can be made regarding the distribution and population size of different bird species. It is essential information to understand why many migratory bird species spending the winter in West Africa are so much in decline.

Many problems associated with relative bird numbers (especially variable detection probabilities) and with averaging bird densities per surface area or habitat type can be solved by focusing on absolute numbers and individual trees. This paper describes the methods we used to obtain absolute bird numbers in individual trees. We substantiate our data collection with information simultaneously recorded on canopy surface and volume of individual trees in combination with species-specific detection probabilities of birds relative to their habitat (tree species, tree condition) and behaviour (selection of micro-habitat, feeding behaviour, vocal activity, flight initiation distance). The results obtained are validated.

METHODS

Study area
Data were collected in 2054 plots across Mauritania, Senegal, The Gambia, Guinea-Bissau, Mali and Burkina Faso between 0° and 17°W and 10° and 18.5°N, from early October to mid-March during 2007–2015. In 1733 randomly selected plots of 300 × 50 m we measured all trees and counted all birds; 321 other plots were selected because of the presence of specific habitat or tree species (for the position of the plots and study design, see Zwarts *et al.* 2015). The northern plots were situated in the southern Sahara (100–200 mm rain/year) with scattered shrubs and few trees. Further south, the landscape gradually turns into heavily grazed woody savanna (annual rainfall 200–500 mm). The usually well-spaced trees facilitated our strategy to consider trees as separate units of study. Further south, the sparse woody vegetation becomes denser, but much of this zone with annually 500–1000 mm of rainfall has been converted into cropland where only a scattering of trees remains, again superbly suited to our method of fieldwork.

Measuring trees
Using Arbonnier (2007), we identified 183 tree and shrub species during our surveys (Zwarts *et al.* 2015). Only three acacias, i.e. *Faidherbia albida*, *Acacia tortilis raddiana* and *A. seyal*, and *Balanites aegyptiaca*, were very common as well as attractive to birds, hence our focus on these tree species in the present methodological study (but we also show data collected in other tree species).

In total, we registered the height and width of 307,914 trees and shrubs (of which only 1.4% was found to contain one or more insectivorous birds). The height of shrubs and trees < 4 m was estimated by eye, but larger trees were measured with a laser rangefinder. The rangefinder was very accurate, but a slanting top of the crown may easily be overlooked when taking the measurement too close to a tree. Consequently, measures with the laser rangefinder were taken at distances of at least twice the height of the tree. Canopy width was estimated by eye as fraction of
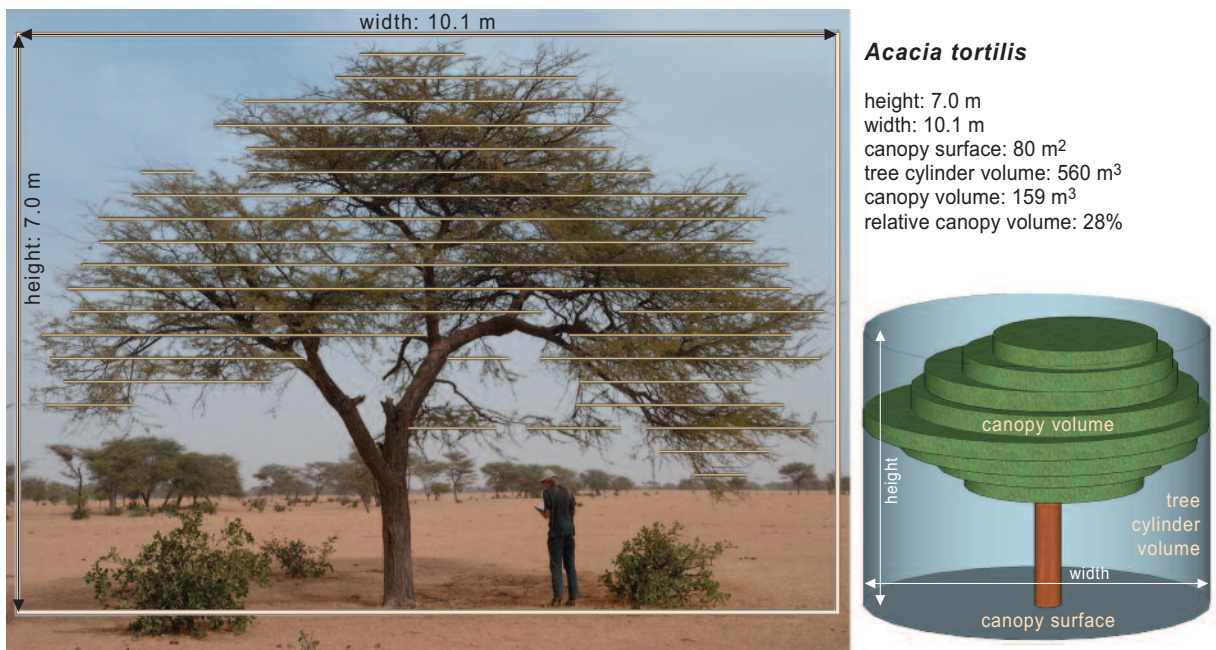
Figure 1. The height (7.0 m) of the tree was measured with a laser rangefinder. Using photos, we measured width, canopy surface (assuming crown was circular) and tree cylinder volume (calculated as product of height and canopy surface). Canopy volume was measured using the grey horizontal lines (see photo), in fact a stack of slices with variable diameter (see drawing) but, if necessary, accounting for gaps in the canopy (see photo). Relative canopy volume is defined as percentage of tree cylinder volume.

the height, but in large trees also by making steps from one end of the crown to the other (steps validated against metres). Many trees were photographed from the position where width and height had been measured. A random sample of 932 photographed trees was selected for further analysis, offering a validation of the field estimate of crown width as fraction of tree height [i]. Width and height of large trees were often measured more than once and from different positions, and multiple photographs taken, to account for anomalies in tree growth and transparency.

The photographs were taken such that the shape of the tree was clearly visible, and these were used to determine canopy width (usually for 10–30 horizontal layers; Figure 1). From these measurements, we calculated *canopy volume*, assuming that the tree canopy is circular [ii]. We did so in two ways: with and without the open patches within the canopy. When open patches were excluded (see Figure 1), total canopy volume was reduced by on average 8%, varying between 0 and 50%. In this paper we use canopy volume after taking into account the open patches within the canopy, i.e. an improved approximation of actual foliage volume available to birds. Canopy volume can be compared to *tree cylinder volume*, i.e. the maximal canopy volume as

determined by measured canopy width and tree height (i.e. from ground level to the top). Since we measured height and width of all trees and shrubs within the plots, canopy surface and cylinder volume are always known, but canopy volume was only calculated for the 665 randomly selected photographed trees (a subset of the 932 photos mentioned earlier).

To understand the relationship between bird numbers and the dimensions of a tree, we need to know more about the shape of trees. Sahelian tree species at first mostly grow in height, later on mostly in width. That is why tree height levels off when plotted against canopy surface (Figure 2A). The canopy volume as percent of the tree cylinder volume differed per tree species, but increased with canopy surface in the four species for which it was analysed (Figure 2B).

The opacity of the canopy may vary independently of the presence of open patches in the crown. In the field we scored the trees regarding their opacity on a 5-point scale: (0) (nearly) leafless, (1) few leaves and open crown, (2) normal transparency of the crown, (3) dense crown, (4) very dense crown (Figure 3). The same was done afterwards using 394 photos. When the field estimate deviated from the estimate based on photographs (in 10% of the trees), the latter was used.
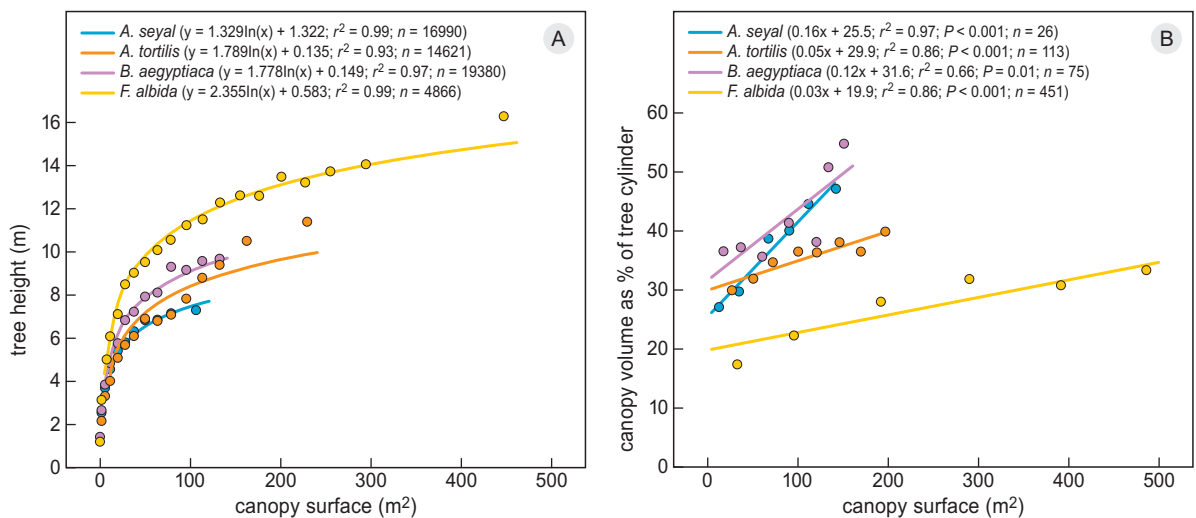
Figure 2. (A) Tree height and (B) relative canopy volume (as percent of tree cylinder) as a function of canopy surface. Explained variance (r^2) and significance (P) refer to average values shown as dots in the graphs. n is total number of trees in which height and width (A) or in addition also canopy volume (B) were measured.

Censusing birds

All measurements regarding trees were done by the same observer (LZ, using a standardized form), whereas at the same time two, sometimes three, other observers focused their attention on the presence, number and identity of birds. Age and sex were recorded whenever possible. For the present methodological study with a focus on Palearctic bird species, we selected insectivorous birds (including African species and species partly feeding on the ground, like Common Redstart *Phoenicurus phoenicurus*) and disregarded roosting ground-feeding birds (doves, starlings, weavers, estrildids, sparrows). We started the observations 10–20 min after civil twilight in the morning and continued till the evening, 10–20 min before civil twilight. We refrained from doing bird counts during the first and last minutes of daylight when many birds were not foraging. All birds were timed the very moment they were detected, to allow comparison of diel variations of density and behaviour relative to civil twilight.

In scrubland, the observers walked parallel courses some 25 m apart, with the record-taker in between. Dense shrub was sometimes beaten with a stick or pelted with cow dung to elicit flight of skulking birds (noting where they went). Trees and shrubs within the plots were approached from various angles, to allow for detection of departing birds as soon as observations started. Each tree was watched simultaneously from opposite sides by two bird observers, starting and ending at the same time, and slowly circling the tree to allow for various views into the canopy. The observa-

tion time was noted as well as the time when the successive birds were detected. Our basic principle was that observations were continued until the observers agreed that all birds present in a tree had been noted (called *observation time*).

We recorded how birds were detected (seen or heard) and whether birds in focus remained silent or started calling or singing during the observation. Of birds seen we noted the height in m relative to ground level (usually validated by tree height as obtained via the laser rangefinder) and whether it was active (usually feeding) or inactive. Inactive birds becoming active, or active birds which became inactive, were noted as active. To prevent over- or underestimating the numbers present, birds leaving the tree during the observation period were noted as present, while arriving birds were not included in the count. Also, bird observers constantly communicated with each other as to birds seen and identified, to avoid double counts or misidentifications.

We recorded aggressive encounters among birds (noting aggressor and victim), as well as prey seen taken by birds during the count. The latter data were biased since large prey with long handling times must be overrepresented. When time allowed, and mostly in between counts so as not to interfere with the census, one of us (RGB), made systematic notes of feeding stations within the tree and foraging methods (using a simplified standardised scheme based on Remsen & Robinson 1990 and Salewski *et al.* 2003); the analysis includes data from Ghana, collected in wooded
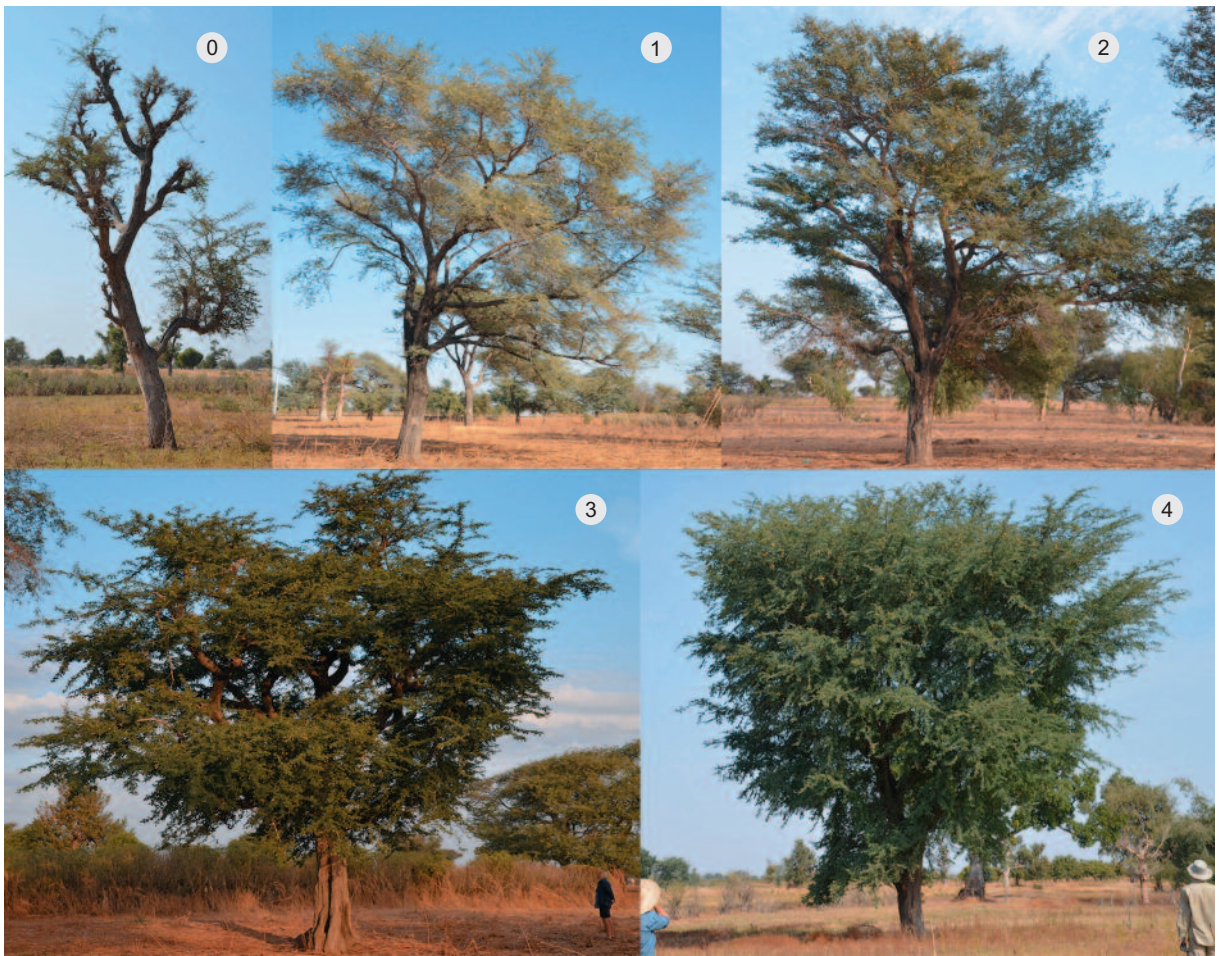
Figure 3. We used a five-point scale (0 to 4) to score the opacity of the canopy in the field and/or afterwards using the photographs, here shown for different *Faidherbia* trees.

savanna in February–March 2009, February–March 2011 and November 2011. Individual birds were followed for as long as possible, from first observation until disappearance from view, resulting in generally short durations of observation [iii]. Pseudo-replication was avoided. Sample sizes were too small to present more than an impression of feeding behaviour (Petit *et al.* 1990). RGB also recorded alert and flight initiation distances of birds (measured in a horizontal plane) when approached directly on foot, counting paces along the way (paces validated against metres) and noting height above ground level (after Blumstein 2006).

In order to relate the observations to air temperature, we collected data from meteorological stations at eight nearby local airports (Bamako, Banjul, Bissau, Diourbel, Mopti, Ouagadougou, Podor, Richard-Toll). The daily temperature is lowest around sunrise and reaches a maximum 7 h later, after which it decreases

to reach the daily average temperature at sunset. This allowed for calculation of temperature per hour for all 234 observation days, using the nearest meteorological station and assuming a linear increase and decline of the temperature in the morning and afternoon, respectively.

SPSS v. 22 was used for statistical analyses; statistical details are given in the endnotes. Logistic regression analysis was performed to test the difference in feeding activity of birds in relation to time of the day, season and temperature. Observation times per tree were analysed with univariate general linear models. Number of birds and canopy surface were noted per individual tree. The measured bird densities per tree are highly skewed because 98.6% of all trees and shrubs held no birds and even in an attractive tree such as *Faidherbia* with one bird per tree, on average, 48% of the trees were devoid of birds. We therefore calculated

the average bird density per tree property (canopy surface, opacity, etc.) before using univariate linear models and (multiple) regression analyses. The analyses were done on the raw data if the number of birds per tree were less skewed (large *Faidherbia*, *A. seyal* on floodplains), but we added logistic regression analyses to test whether the presence of birds in trees was related to tree-related variables as bird numbers were still not normally distributed.

Bird names are according to the BirdLife Checklist Version 7.0. Western and Eastern Olivaceous Warblers *Hippolais opaca* and *H. pallida* were lumped, as were Common and Iberian Chiffchaffs *Phylloscopus collybita* and *P. ibericus*.

RESULTS

Tree-specific time budget of the observers

Observation time increased with canopy surface, although the function differed per tree species (Figure 4) [iv]. Observation time showed a linear increase with canopy surface (Figure 4), but levelled off when plotted against canopy volume, as shown for *Faidherbia albida* (Figure 5A). Hence, time spent per unit cubic metre decreased with *Faidherbia* size, on average from 2.4 to 0.6 m^3/s for canopy volume and from 8 to 2 m^3/s for tree cylinder volume. As expected, observation time increased with number of birds present (Figure 5B). On average, it took 110 s for each additional bird to be detected. However, there are more birds in large trees and trees with a high opacity score. When controlled for these two factors [v], the increase of observation time with number of birds (varying between 0 and 17 with no bird in 48% of *Faidherbia* trees and 1 bird per tree
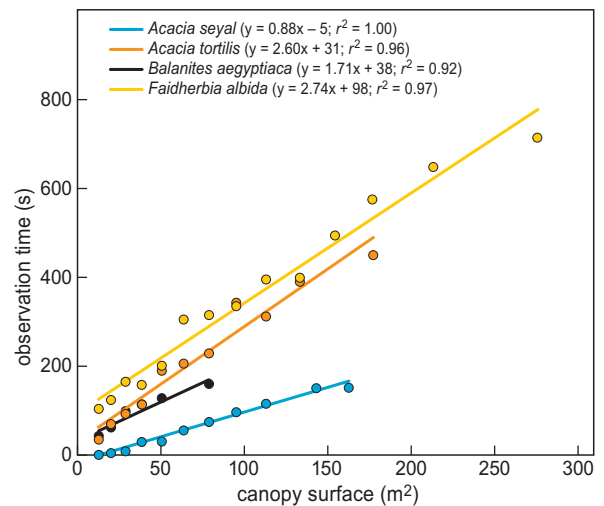

Figure 4. Time taken by two observers to detect birds in four tree species of different canopy surface. The regression lines are calculated over the averages per category (4, 5, 6, … 20 m canopy width). Regression equations and explained variance (r^2) are shown; all equations are highly significant ($P < 0.001$); further details in endnote [iv].

on average) was reduced from 110 to 75 s/bird, still highly significant (dashed line in Figure 5B). The impact of crown opacity (Figure 5C) on observation time was large and was hardly reduced when canopy volume or number of birds were taken into account.

The observation time per tree for two observers varied between 1 s for a bare shrub and 2502 s for a large tree with a dense canopy. This variation may be explained by several intercorrelated variables. A statistical analysis [vi] revealed that the observation time depended on seven variables: canopy width, opacity and number of birds and, to a lesser degree, tree height,
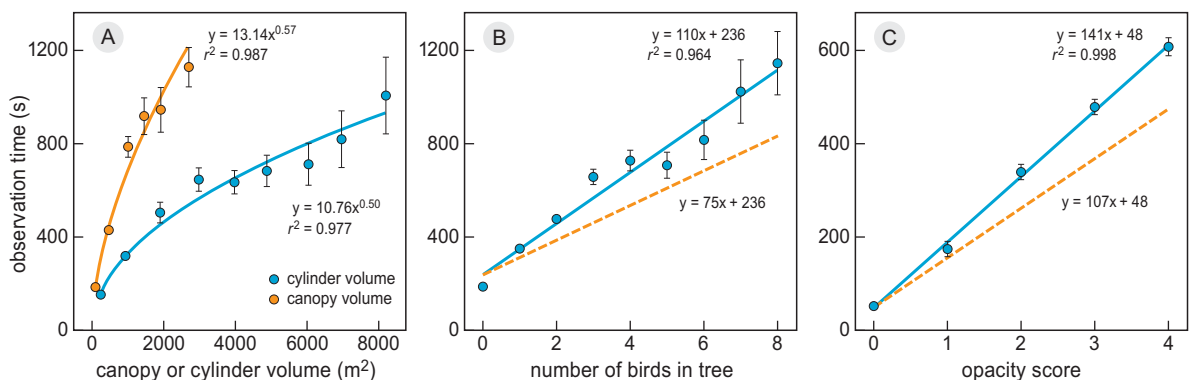

Figure 5. Observation time (±SE) for birds in *Faidherbia* trees as a function of (A) tree cylinder volume or canopy volume, (B) number of birds in a tree and (C) opacity score. The equations and the explained variance (r^2) are shown. The average values were calculated for 1159 trees (except for canopy volume, where $n = 429$). The dashed lines in figure B and C account for the effect of both other variables; further details in endnote [vi].
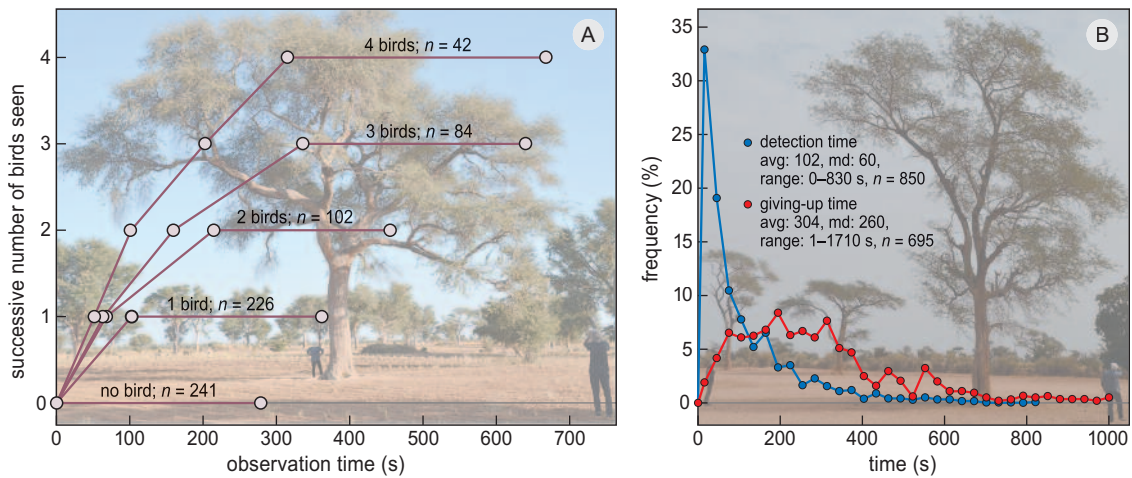
Figure 6. (A) The time it took for two observers to detect successive birds in a *Faidherbia* ('detection time'), given separately for trees in which 0 to 4 birds were detected. The horizontal lines show how long the observation was continued after the last bird had been noted ('giving-up time'). A selection was made of *Faidherbia* with a canopy width of at least 11 m; *n* = number of trees; further details in endnote [viii]; (B) Frequency distribution of detection and giving-up times; based on the data given in (A).

tree species, month and year. From this we conclude that (1) observation time is determined more by canopy surface than by tree height, (2) differences in observation time between tree species (Figure 4) largely disappear when number of birds and opacity are taken into account, and (3) differences between months and between years largely disappear when canopy surface, opacity and number of birds are taken into account. The latter is an indication (but no proof) that our searching effort has been more or less constant across the observation period.

The implicit decision rules regarding the time required to detect all birds in a tree became clear when the detection time of successive birds was plotted against the observation period per tree (Figure 6A). Since observation time varied per tree size, for use in Figure 6 we selected only *Faidherbia* trees with a crown width of 11 m or more. When birds were absent, the observation was ended, on average, after 295 s. When a single bird was recorded, it was, on average, detected after about 100 s, after which the observations were continued for another 300 s, on average. When a tree held more birds, the total observation time increased with the number of birds seen. This was partly due to the fact that the discovery of another bird needed a check against a bird or birds seen earlier on, to exclude double counts, especially imperative for species with little or no sex- and age-differences such as *Phylloscopus* species. Independent of how many birds were detected, the observations were continued for, on average, another 300 s after the last bird was noted, which may

be considered as the giving-up time. The giving-up time was, on average, three times longer than the average detection time and the difference is even larger when the median is compared: 60 s for detection time and 260 s for giving-up time (Figure 6B). Perhaps surprisingly, giving-up time of the observers was independent of the number of birds detected in the tree, but increased with canopy surface from less than 20 s in a small tree to over 400 s in large trees (Figure 7) [vii].
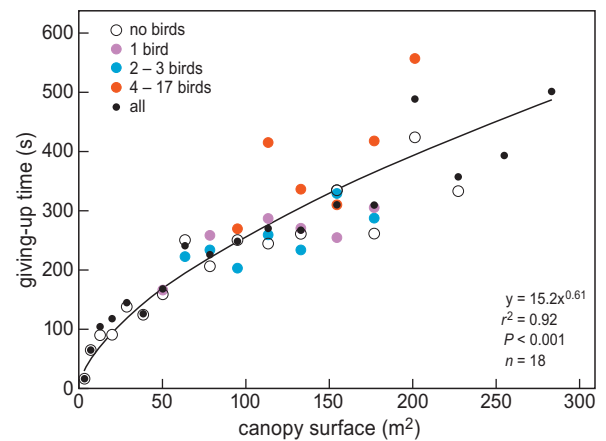

Figure 7. The giving-up time of two observers searching for birds in a *Faidherbia* tree as a function of its canopy surface. The regression line refers to 18 categories (2–19 m canopy width) for which the average giving-up time was calculated; total *n* = 1097. Symbols show the average giving-up times depending on the number of birds seen (if *n* > 10); giving-up time was independent of bird numbers, as also shown in endnote [vii].

The variation in detection and giving-up times was large (Figure 6B), partly because trees differed in size (Figure 5A) and opacity (Figure 5C; see also endnote [vi]). There are additional reasons why the giving-up time was so variable. Very short giving-up times sometimes occurred when extra time was needed to identify a bird or to be sure about the number of birds. For example, a bird may elude identification for quite some time, but when it finally received a name the tree had been scanned so thoroughly that further observation had become superfluous (hence stopped abruptly, accounting for the unusual giving-up time of 1 s). Similarly, the giving-up time was short if after a while it was decided there were, for instance, three and not two Bonelli's Warblers *Phylloscopus bonelli* in a tree. Would the decision in this case had been two birds, the giving-up time would have been long.

It is important to note that the analysis of detection and giving-up times was done afterwards, i.e. not during the years when the data were collected. The apparent giving-up time, as shown in Figures 6 and 7, is therefore independent of the outcome of the analysis. It can be seen as a rule of thumb of the various observers striving not to miss any birds.

Generally, the time needed to discover successive birds in a tree progressively increased from the first to the last. How many birds would have been overlooked at shorter observation times is difficult to say. However, an estimate can be made by analysing the timing of detection of birds in the timespan that a tree was scanned (Figure 8). On average, 81% of the birds were detected in the first half of the observation time, varying from 88% in Beautiful Sunbird *Nectarinia pulchella* to 69% in Common Whitethroat *Sylvia communis*. Of Bonelli's Warblers, 62% were observed in the first quarter of the observation period against 11%

in the last quarter. This difference was much smaller for Common Whitethroat, where 31% and 21% were respectively detected in the first and last 25% of the observation time. These data suggest that for shorter observation times the risk of missing a Common Whitethroat was larger than for a Bonelli's Warbler.

Bird behaviour, tree properties and detectability

Detectability of birds was largely species-specific, depending on where they foraged (Figure 9A) and how (Figure 9B). The Orphean Warbler *Sylvia hortensis* was the most secretive bird, foraging on trunks, branches and twigs. This was also true, to a lesser degree, for the two other *Sylvia* species (Subalpine Warbler *Sylvia cantillans* and Common Whitethroat) and for Olivaceous Warbler (Figure 9A). In contrast, other species were relatively easy to detect. Common Redstarts usually foraged on bare ground beneath a tree (pouncing from low branches), while *Phylloscopus* species foraged among leaves and flowers and were usually flitting around on the outside of the trees.

The detectability of birds also clearly related to foraging behaviour (Figure 9B). A sallying, hovering, or jump-flighting bird is difficult to miss in contrast to a stationary or slow-moving bird pecking prey from a branch. Due to its behaviour, the Orphean Warbler was again the most difficult species to detect, being a well-hidden slow mover with immobile intervals. The other *Sylvia* species were also sneaky birds in contrast to the agile *Phylloscopus* species. Bird species with conspicuous foraging techniques occurred on average in more open feeding strata, and vice versa (Figure 9A, 9B). The observations summarised in Figure 9 explain why it took, on average, more time to detect a Common Whitethroat than a Bonelli's Warbler (Figure 8).
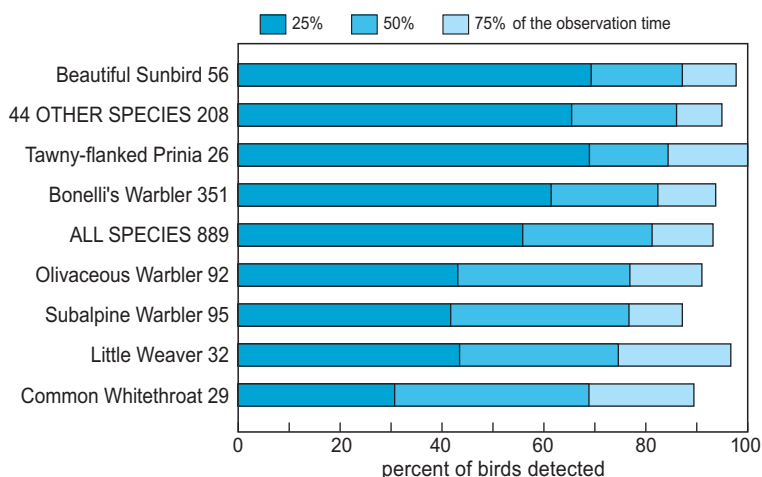

Figure 8. The percentage of birds being detected within 25%, 50% and 75% of the total observation time, for the seven most common species (with *n*). The other 44 species have been lumped. Bird species are ranked according to the median. A selection is made of large *Faidherbia* (on average 12.4 m high and 15 m wide; *n* = 321), with an average observation time per tree of 596 s.
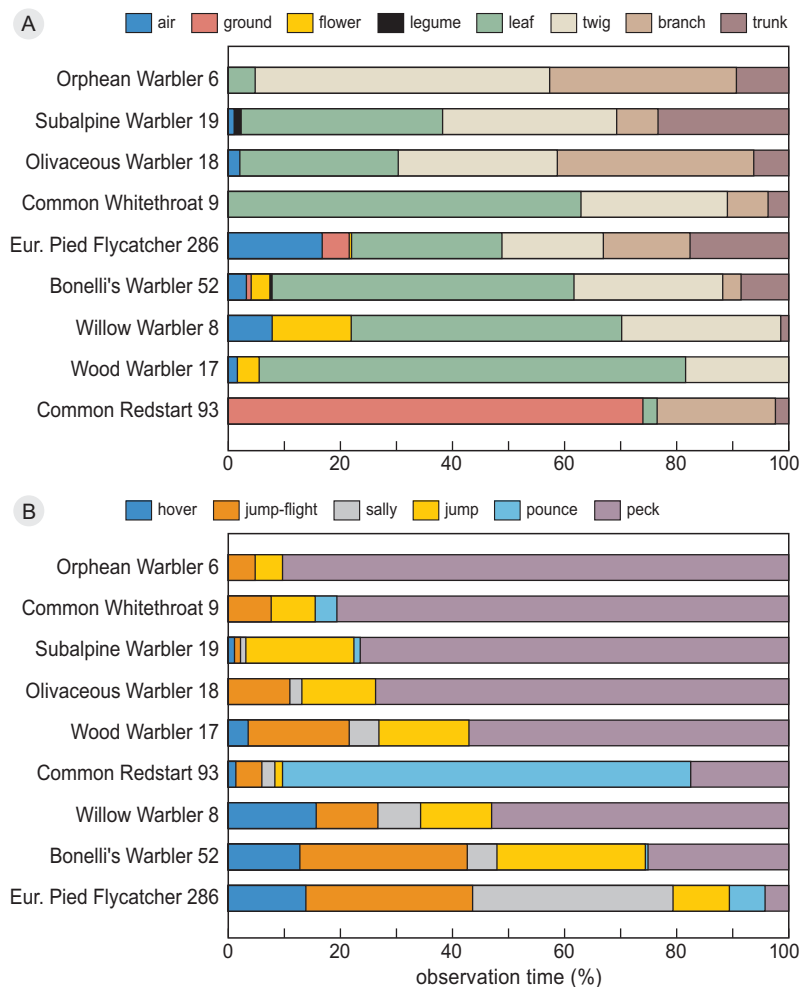
Figure 9. The time (%) spent in (A) eight different microhabitats and (B) using seven different feeding techniques. Habitats and feeding techniques are ranked from left to right according to detectability of birds (from high to low). The order of the species from top to bottom is determined by their detectability (from 'difficult' to 'easy') in terms of microhabitat or feeding techniques. Total observation time: 514 minutes (337 observation periods of, on average, 91 seconds). The observation time (min) per bird species is given.

Between birds foraging in Sahelian trees, aggressive encounters were rife, which helped in locating birds. In particular, Olivaceous Warblers spent lots of time chasing birds, usually other species, out of the tree, often accompanied by calling and bill rattles. Intraspecific aggressive interactions were frequent between Subalpine Warblers when a tree held more than a single one. Bonelli's Warblers were always on the receiving end of aggressive encounters with Olivaceous and Subalpine Warblers.

Feeding or aggressive birds were rather easy to detect. Detection became more difficult when birds were inactive, notably when residing in a dense crown. However, the incidence of inactivity showed a wide variation across species. We never recorded an inactive

Chiffchaff or Senegal Eremomela *Eremomela pusilla* and very few resting Bonelli's Warblers (Figure 10). In contrast, about 15% of European Pied Flycatchers *Ficedula hypoleuca* and Common Redstarts were scored as inactive, partly due to their habit of foraging as sit-and-wait-predators (especially Common Redstart); Pied Flycatchers definitely had a noon lull in their time budget in wooded savanna (Janne Ouwehand & RGB unpubl.).

The proportion of inactive birds tended to increase, but non-significantly, with air temperature (varying between 14 and 41°C) in Bonelli's Warbler and Subalpine Warbler; in other bird species no such trend was evident [ix]. The fraction of inactive birds varied slightly during the season, increasing from 4–6% in October/
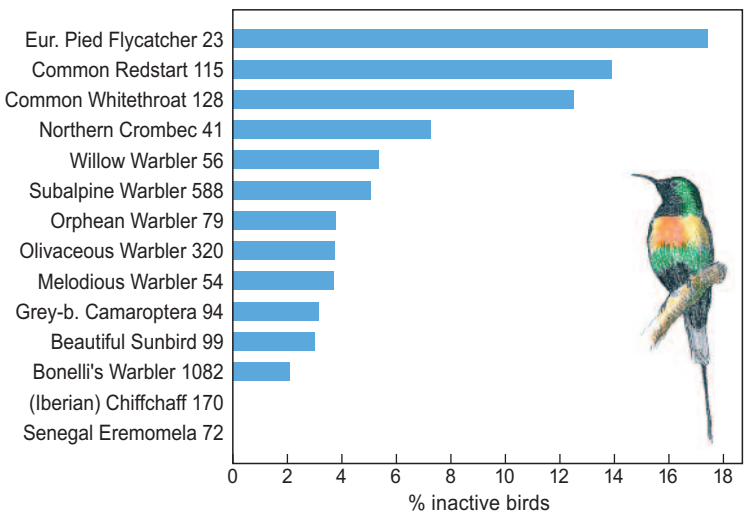
Figure 10. The percentage of inactive birds in 14 species (total $n = 3055$, with numbers given per species.

November to 9–10% in December/January and decreasing afterwards to 6–7%, but this seasonal variation was not significant for the different bird species[x]. During the day, the activity pattern varied little, albeit with fewer inactive birds in the early morning and late evening and more around noon; the diel variation in activity pattern was larger in Bonelli's Warbler than in other species[xi]. Remarkably, 38% of the Subalpine Warblers (8 of 21) in *Salvadora persica* were inactive – probably due to feeding limits set by a digestive bottleneck (Kersten 1996) related to the diet of berries –, against 4% (22 of 535) in other trees where they foraged on insects. These data suggest that insectivorous birds in the Sahel have to work hard throughout the daylight period. The question remains, however, to what degree the low percentage of inactive birds is due to quiet birds remaining unnoticed.

Singing and calling birds are difficult to miss when the observers stand close to a tree, even considering the fact that midwinter-song in migrants was usually voiced as subsong, a soft warbling sound. 55 to 100% of the birds were detected by eye (Figure 11), of which a small fraction started singing or calling after they had been detected. More than half of the birds would have been missed if they had been solely located by ear.

In early morning, the fraction of birds vocalizing was highest but it decreased gradually in the course of the day (Figure 12). Bonelli's Warblers showed an early morning peak in vocal activity (Figure 12B), whereas Subalpine Warblers had a distinct early morning peak
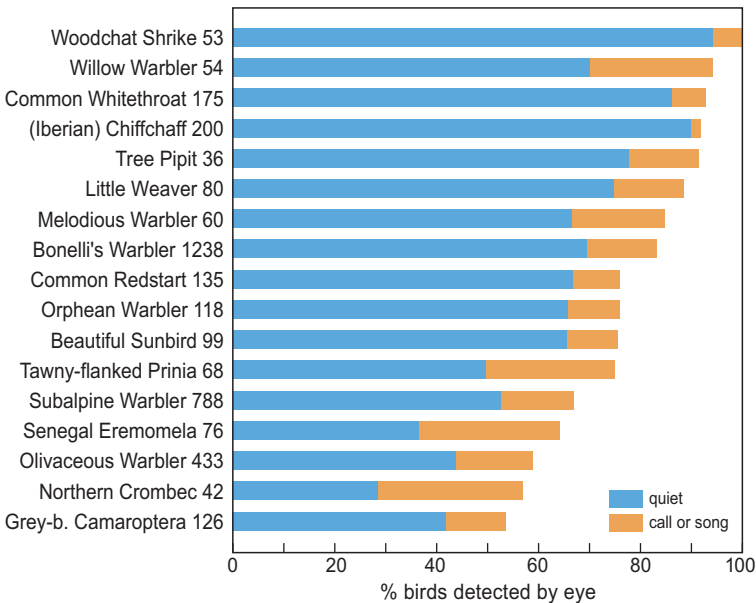

Figure 11. The percentage of birds detected by eye. Most birds remained quiet during the observation period (blue), but some started calling or singing later on (brown); all other birds were detected by ear. Total $n = 3781$; number per bird species indicated; species selected with $n > 35$.
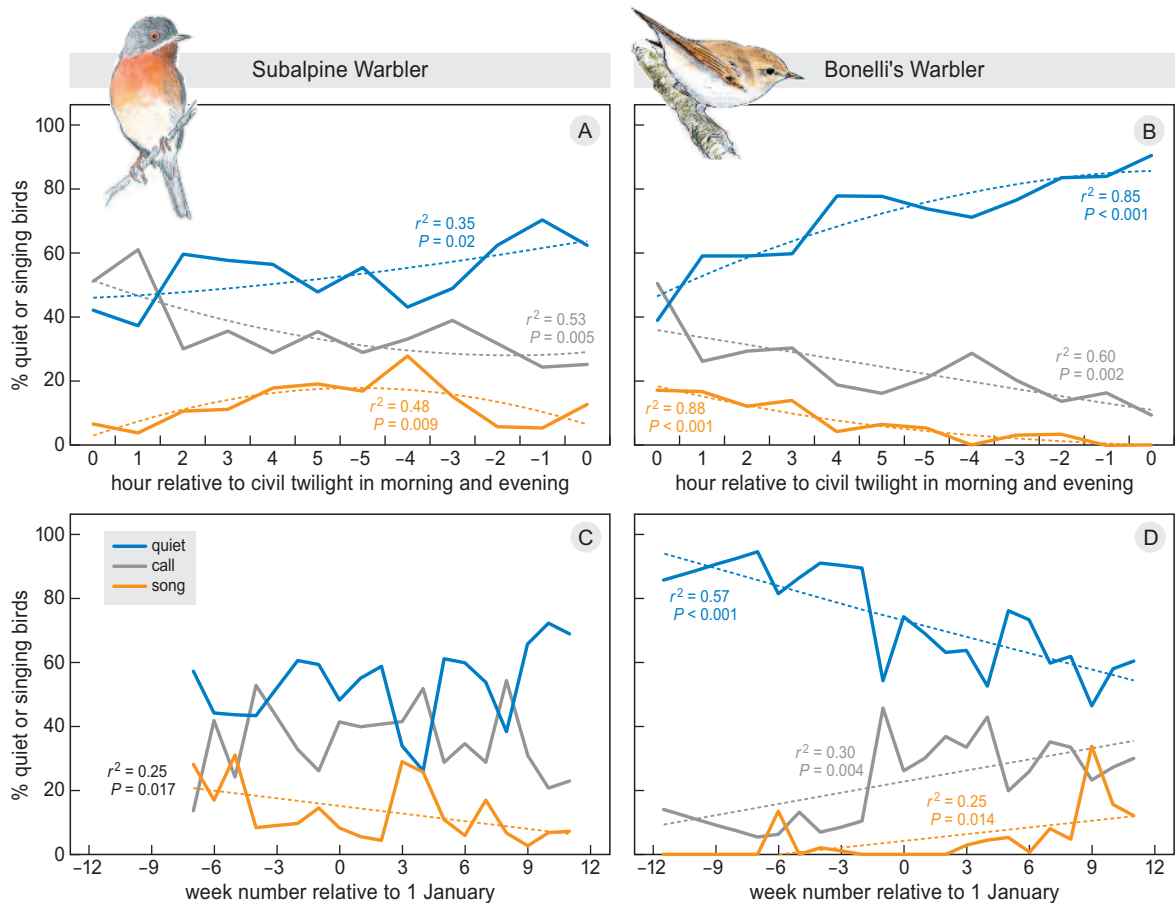
Figure 12. The variation in the percentage of silent and singing Subalpine Warblers (left) and Bonelli's Warblers (right) in the course of the day (upper panels) and during winter (lower panels). r^2 and P refer to the regression lines (shown when significant); more details in endnote [xii].

in calling, but sang most often just after noon (Figure 12A). We expected song activity of migratory species to increase in the course of the winter season, especially prior to migration. This change was indeed found in Bonelli's Warblers (Figure 12D), but the trend was reversed in Subalpine Warblers (Figure 12C).

Detectability of birds also depended on their flight distance. *Phylloscopus* species were easy to approach without eliciting a flight response, in contrast to *Sylvia* species, Common Redstart, Pied Flycatcher and Woodchat Shrike *Lanius senator* (Figure 13A). Species-specific differences in flight distance (measured in a horizontal plane) can partly be explained by the height at which the birds were seen. *Sylvia* species high up in a tree were easier to approach than the same species lower in the tree or in shrubs, although not as close as *Phylloscopus* species. The largest flight distances were recorded for birds present in the lower part of the trees or in shrubs, albeit not as large as species feeding on the ground (Figure 13B). As most birds were present in

the upper part of trees (although only 18.6% of the investigated trees and shrubs were > 4 m high, 79.3% of the birds were seen > 4 m above the ground), bird counts usually did not result in observer-induced flight. In fact, walking below and around large trees was possible without disturbing the birds. In contrast, birds often departed from shrubs at our approach.

How many birds remain undetected?
Our bird counts covered the entire day, almost from dawn to dusk. If substantial numbers of silent or inactive birds had been missed, the observed average density would have varied in the course of the day. However, we failed to find consistent or significant diel variations in bird density [xiii]. A crude effort to check the validity of our estimate of absolute numbers was made on 8 and 9 March 2015, when we selected 6 large *Faidherbia* (in a field with 50) to count the birds in late evening, early next morning and around noon. We recorded 10, 13 and 11 birds respectively, with slight
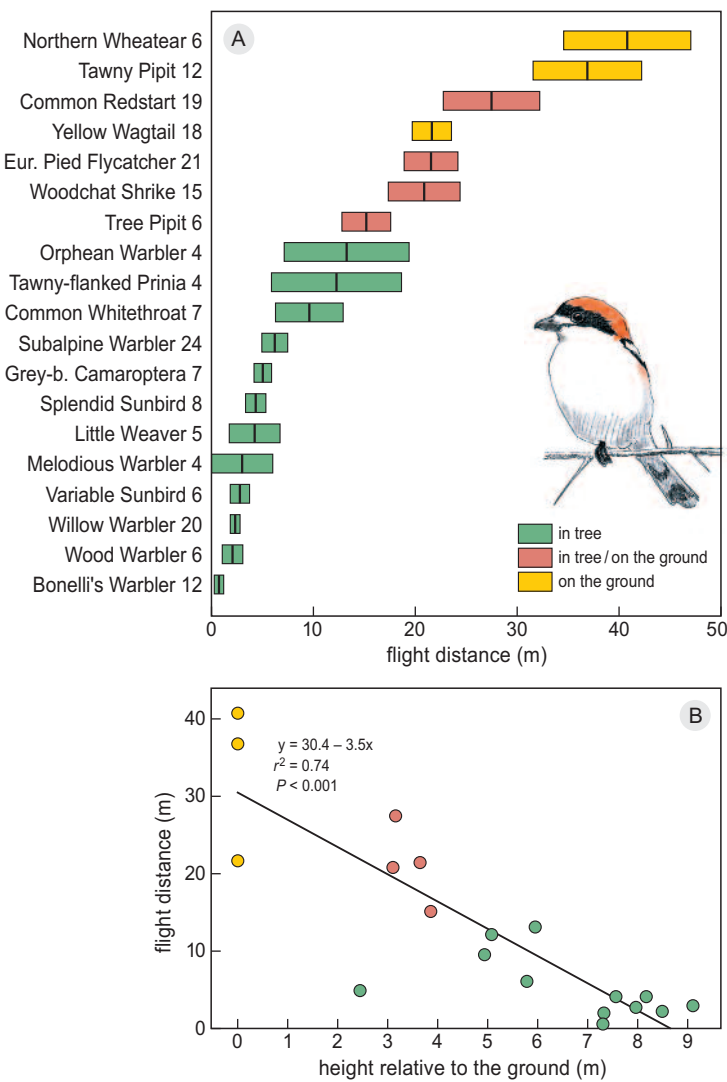
Figure 13. (A). Flight distances (m ± SE) measured in a horizontal plane in 19 bird species, foraging in trees, on the ground or both. Number of observations varied from 4 in three bird species to 24 in Subalpine Warbler; total n = 204. (B) Flight distance as a function of average height in the tree at which bird species were noted (m above the ground); same species as in (A); average heights are taken from Figure 4 in Zwarts *et al.* (2015).

variations in numbers per species probably due to movements of birds between trees (e.g. 1, 2 and 1 Subalpine Warbler, 5, 7 and 7 Bonelli's Warbler, 2, 1 and 1 Common Whitethroat, respectively). Another way to validate detection probability is to compare the fraction of birds detected by eye in tree species of different opacity. If a higher proportion of birds were detected by ear in dense tree species, such as *Balanites aegyptiaca*, compared to trees with a transparent crown, like *Acacia seyal*, this might indicate that more birds had been missed in dense trees. Again, the analyses revealed no such obvious difference [xiv].

The question remains whether more birds would have been seen if the observation time per tree had been prolonged. This was checked by doing the bird count as usual, then pelting the tree with stones or shaking branches to flush any remaining birds after the observation time. During the northern winter, most Sahelian trees have a rather transparent crown or are (nearly) leafless, providing a clear view into the canopy most of the time. Our check was therefore restricted to dense shrub and trees (estimated at <10% of the woody vegetation) in which inactive birds were most likely to have been overlooked.

In total, we detected 54 birds in 321 dense trees and shrubs during the timed observation period and another three birds afterwards (Table 1). When the air temperature varied between 13 and 32°C, none of the 32 birds were missed in 297 trees, but at higher temperatures (up to 41°C), 3 out of 25 birds (12%) remained undetected. The three undetected birds must have been immobile and probably in deep shadow. The missed birds were recorded during hot, windless days with a ground temperature in the full sun of up to 61°C,

inductive of inflicting hyperthermia as evident from birds panting with open beaks.

Taking all data and validations together, we conclude that our census effort was sufficiently reliable to obtain absolute bird numbers: we missed at most a few percent of the birds in trees and shrubs with a dense crown (less than an estimated 10% of the woody vegetation) and none in shrubs and trees with an open crown.

Converting counts into densities

It would simplify our study if bird density in trees could be expressed as number per canopy surface. However, the numbers of foliage-gleaning birds are more likely to be a function of foliage biomass and thus canopy volume. Nevertheless, we found that the number of birds depended on canopy surface. Taking canopy surface into account, tree height was less, or even not, statistically relevant. This is borne out by multiple regression analyses for different tree species where bird numbers were regressed against canopy surface and tree height [xv].

Assuming that bird numbers in a tree are not related to tree height, but to canopy surface, we may use the average density per canopy surface as the simplest predictor of bird numbers per tree. In *Faidherbia* trees we noted, in total, 2400 tree-dwelling birds in 25,768

Table 1. Total number of birds detected in 321 shrubs and trees (height, on average, 6 m, range 1–14 m, taller trees were disregarded as we did not feel confident to be able to flush birds in trees higher than 14 m), all with a dense crown (*Balanites aegyptiaca*, n = 223; *Acacia tortilis*, n = 30; *Faidherbia albida*, n = 20; *Diospyros mespiliformis*, n = 20) and 10 other species (with 1 to 7 trees each), split up for birds detected during the standard procedure, and missed birds that were flushed afterwards. The data were collected during 27 days between mid-November and mid-March.

Species	detected	missed
Subalpine Warbler	10	0
Bonelli's Warbler	10	1
Grey-backed Camaroptera	2	0
Northern Crombec	2	0
Common Whitethroat	1	1
Orphean Warbler	2	0
Tawny-flanked Prinia	4	1
Woodchat Shrike	2	0
Olivaceous Warbler	3	0
Little Weaver	3	0
other bird species	15	0
Sum	54	3

ha canopy, resulting in an average density of 93.1 birds/ha canopy. For *A. seyal* this was 33.6 birds/ha, for *A. tortilis* 54.2/ha and for *Balanites* 43.7/ha. Figure 14 shows the expected number of birds depending on canopy surface based on the average densities mentioned earlier, hence assuming that the bird density did not vary with canopy surface. A better fit is obtained, however, if we take into account that bird density increased with canopy surface (shown as dashed line in Figure 14) [xvi]. The difference is small, except in *A. seyal*, a tree species in which the density in small trees (surface < 10 m^2) amounted to 9.4 birds/ha against 48.2/ha for larger trees.

Alternatively, we also modelled bird numbers for a three-dimensional space. We calculated for each tree the summed canopy as tree cylinder (multiplying canopy surface and tree height, using the equations given in Figure 2A). For *Faidherbia*, we then arrive at 1.5 birds/1000 m^3, slightly higher numbers in *A. tortilis* but fewer in Balanites (1.4/1000 m^3) and *A. seyal* (1.0/1000 m^3). The yellow line in Figure 14 gives the predicted number of birds if the average density per m^3 would not vary with canopy surface. In all four tree species the fit is no improvement compared to the two-dimensional model.

This three-dimensional model is too simple, however, because relative canopy volume (i.e. as percent of canopy cylinder) increases with canopy surface (Figure 2B). If the regression equations given in Figure 2B are included in the model, we arrive, on average, at a density varying between 3.3 birds/1000 m^3 canopy volume in *A. seyal* and 6.5/1000 m^3 in *Faidherbia*. The grey line in Figure 14 gives the predicted relationship with canopy surface, based on these average numbers per m^3 canopy. The fit is better in all four trees compared to the model based on a tree cylinder, but still very poor for *A. tortilis* and in the three other species not better than the regression equation fitted on canopy surface.

One might expect an increase of bird numbers proportional to canopy volume only if birds exploit the full canopy during foraging. However, if birds are more partial as to their foraging niche within a tree, for instance only the exterior part of a tree with flowers, a linear relationship is to be expected between bird numbers and canopy surface. Feeding niches have not been quantified during our surveys, but in general *Sylvia* species and Olivaceous Warbler were found more often foraging in the inner part of the crown than *Phylloscopus* species (Figure 9A), making it worthwhile to repeat the analyses, as shown in Figure 14, separately for the different bird species. The density of
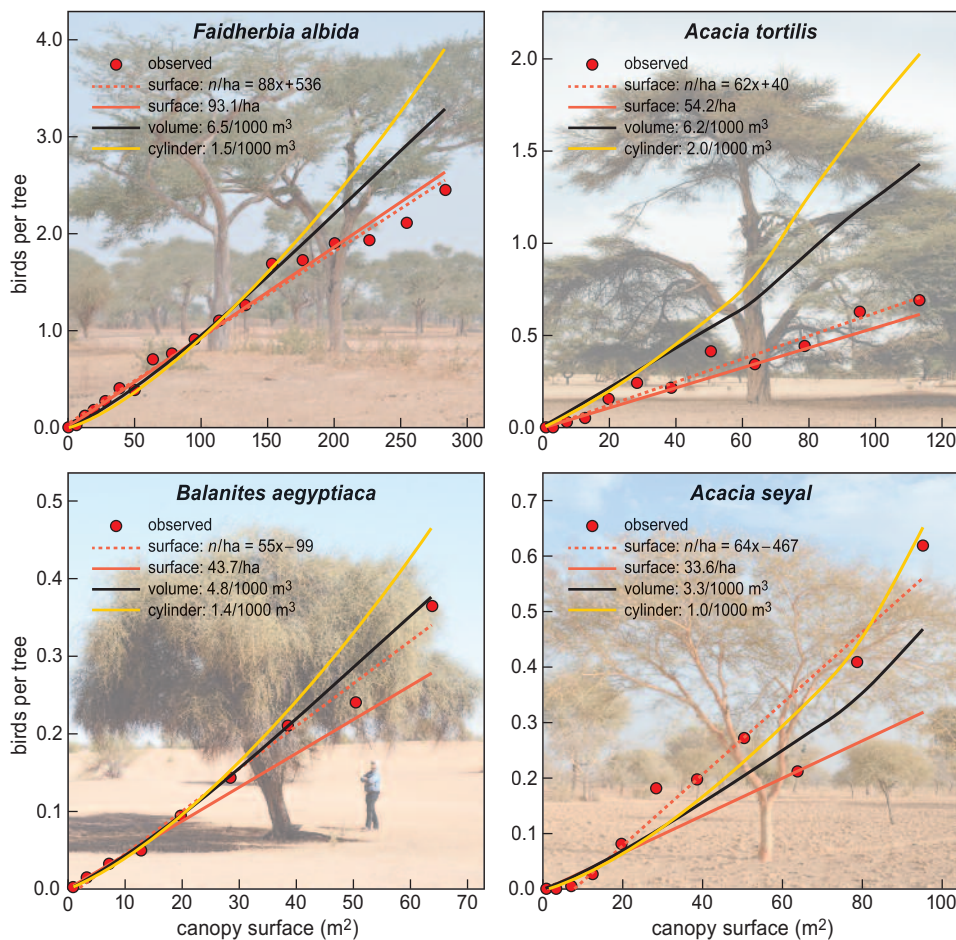
Figure 14. Average number of birds observed in a tree as a function of canopy surface (dashed line), compared to expected number assuming the average number of birds per canopy surface or per canopy volume is constant for trees with a different canopy surface. The expected number as a function of tree cylinder and canopy volume is derived from equations given in Figure 2.

Bonelli's, but also Subalpine Warbler, then appeared to be a function of canopy surface. The fit does not improve when bird numbers are plotted against canopy volume. In contrast, the density of Olivaceous Warbler seemed to be mostly related to canopy volume. However, this species did not occur in small trees (canopy surface < 10 m^2). When small trees were disregarded, the density of Olivaceous Warblers was also related to canopy surface. The same applied to other species only found in larger trees: Common Redstart and Orphean Warbler.

The main conclusion of this exercise is that bird density can be reliably expressed as number per canopy surface taking into account that the density per surface area increases with canopy surface. However, note that the average values in Figure 14 are derived from substantial samples and that the variation in density is large.

Food and bird densities in trees

Given the almost nonstop activity of birds from dawn to dusk, food supply is expected to be a major factor in explaining bird densities in trees. As the average density of insectivorous bird species in the 183 woody species in our survey varied between 0 and 130 birds per ha canopy surface, depending on tree species (see appendix in Zwarts *et al.* 2015, for details) and season, variation in food supply must be substantial. However, we did not quantify food abundance, except for some proxies and anecdotal observations.

In *Faidherbia*, bird density increased with the number of flowers in a tree [xvii]. We also expected more birds in trees with a dense canopy (using opacity score as a rough estimate of foliage volume); the fit was especially close in *Faidherbia* (Figure 15A). In *Faidherbia* we found that bird density per ha canopy not only depended on opacity but also on canopy volume
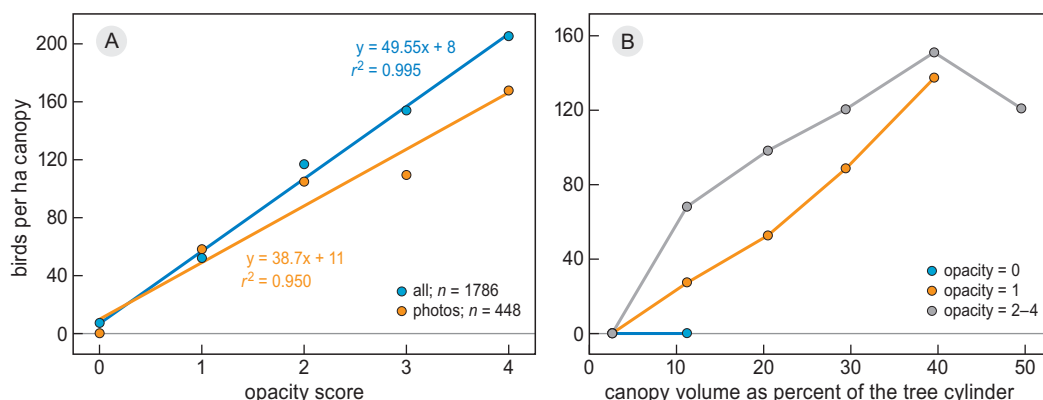
Figure 15. Bird density per ha canopy in *Faidherbia* as function of (A) opacity score, such as measured in the field and/or calculated from photographs, or (B) using only photographed trees where canopy volume is expressed relative to tree cylinder volume for three categories of opacity; statistical details in endnote [xviii].

as percent of cylinder volume (i.e. relative canopy volume, which in *Faidherbia* varied between 7 and 58%). There were no birds in *Faidherbia* when relative canopy volume was less than 5% but it increased to 120–150 birds per ha in trees with a full canopy and a relative canopy volume amounting to 40–50% (Figure 15B). The highest densities were found in trees with a full canopy and a high opacity.

Other observations suggested that large variations in bird density per tree may be explained by variations in food supply. For example, we noted that all bird species in *Faidherbia* and other *Acacia* trees took caterpillars and moths. In *Faidherbia*, we found a cryptic moth species, probably *Crypsotidia* spp., to be abundant and preyed upon by the birds present. Since the lowest branches were usually out of reach, we estimated moth density by counting the number of moths hidden in cracks in the bark. Moths were flushed by three times striking the trunk at breast height. Bird density showed a correlation with this indirect measure of food density (Figure 16). Its biological significance, however, is uncertain, since we have no data on how moth abundance related to caterpillar numbers. The foraging technique of the three *Phylloscopus* species, especially hovering and jump-flights, favours the catching of moths (8 moths taken vs. 24 caterpillars), at least more so than in the slow-moving *Sylvia* warblers (2 vs. 27). In fact, several times we recorded Bonelli's and Wood Warblers *Phylloscopus sibilatrix* fluttering against the tree trunk and chasing flushed moths. The density of *Phylloscopus* species, but also of all other species combined, increased with number of moths flushed from *Faidherbia* trunks (Figure 16), suggesting that moth abundance might be a reliable indicator of caterpillar abundance.

Insect outbreaks may attract birds to trees which would otherwise have been without birds. Two anecdotal observations, of high insect abundance in Néré *Parkia biglobosa* and in Cashew *Anacardium occidentale*, are illustrative. We checked a total of 396 *Parkia*, in which we recorded 18 birds, including 3 Chiffchaffs and 2 Tree Pipits *Anthus trivialis* that used the tree as perch to find food on the ground below. Of the remaining 13 insectivorous birds, six were detected in a single tree; in seven trees we saw one bird and none in the remaining 386 trees. When we approached the only bird-rich *Parkia*, it was abundantly clear from a distance that the colour of the leaves differed from normal. The leaves proved to be covered with lice and we saw that 3 Senegal Eremomelas, 2 Bonelli's Warblers and 1 Pied Flycatcher were frenetically feeding on this small prey. We counted 80 (20–150, $n = 25$ leaves) lice per leaf and estimated the number of leaves for this
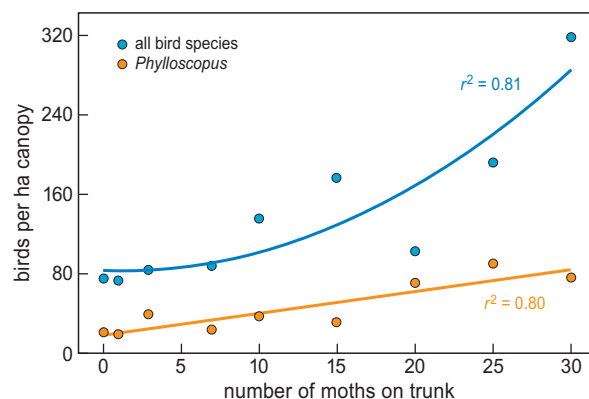

Figure 16. Birds per ha canopy in *Faidherbia* as a function of the number of moths flushed from the trunk at breast height. Statistical details in endnote [xix].
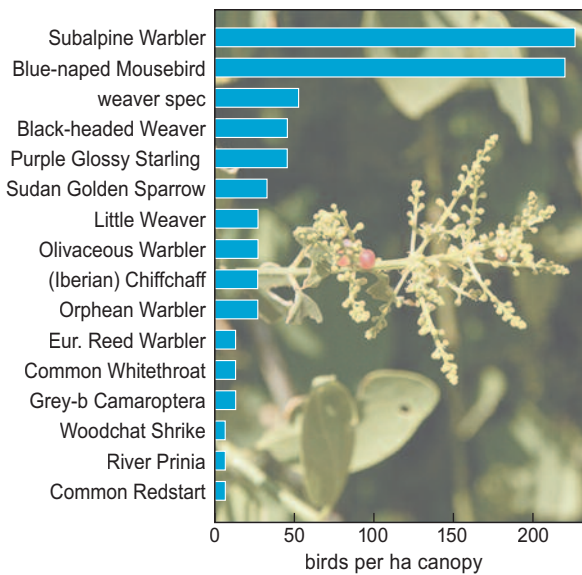
Figure 17. Birds per ha canopy in *Salvadora persica* if berries were present (based on 1497 m^2 canopy; total density 795 birds/ha). In shrubs without berries we only saw two birds, a (Iberian) Chiffchaff and a Common Redstart (3651 m^2 investigated; 5 birds/ha).

relatively small tree (10 m high and 9 m wide) at 150,000, home to an estimated 10 million lice. Whenever possible, we checked other *Parkia* trees for the presence of lice on leaves, but never encountered anything like it. A similar case was recorded for Cashew trees, where overall bird density was also extremely low: in 2590 trees we recorded no birds at all, in seven trees one bird and in one tree two birds. The leaves of the latter tree were rich in lice.

Many insectivorous bird species may temporally become frugivorous. In fact, we recorded the highest bird density in a shrub species, *Salvadora persica*, where insectivorous birds do not feed on insects but on berries. This shrub harboured, on average, 95 insectivorous birds/ha canopy and another 86 seed-eating birds/ha canopy, taking all observations from early October to mid-March together. When a selection is made for shrubs with berries, the average bird density in *Salvadora* amounted to 367 insectivorous birds/ha and 795 birds/ha including seed-eaters. In contrast, there were only 5 birds/ha when *Salvadora* had no berries (Figure 17). The variation in food supply per shrub is clearly huge and this explains much of the observed variation in bird density. In Salvadora, food supply can be measured easily, counting the bunches (varying between 0 and 6000 per shrub; on average 1123; $n = 33$), the number of berries per bunch (on average 92, varying between 35 and 186), and the

fraction of ripe berries (on average 0.08%, varying between 0 and 6%; all data from NW Senegal in October). Thus, although food supply in *Salvadora* is potentially enormous (see also Stoate & Moreby 1995), no more than 2.7 ripe berries per m^2 were at the birds' disposal in October. Still, it apparently sufficed to attract many birds, to such an extent that ripening berries were constantly being depleted. As in *Salvadora*, very few birds were present in *Zanthoxylum zanthoxyloides* unless berries were available. In this species, 6 birds were recorded in a single shrub, 1 in another and no birds in 59 remaining shrubs. The shrub with six birds was the only one recorded with ripe berries during our surveys.

Bird density in trees varied seasonally due to the variation in the amount of leaves and flowers. This can be illustrated with data collected for *Acacia seyal* in a plot in the floodplain of the Inner Niger Delta in November and February. Bird density in February was twice as high as in November (107 vs. 55 birds/ha canopy). In November, not more than 8% of the trees carried flowers, against 79% in February. Also the foliage volume differed. In November, 24% of the trees were bare, against 14% in February. If bird density in both months were to be calculated for trees with a similar opacity and the same number of flowers, the seasonal differences in bird density largely disappeared[xx]. In both seasons, few birds visited bare trees, but bird density increased to 300–400 birds/ha canopy when trees had a dense canopy and carried more than
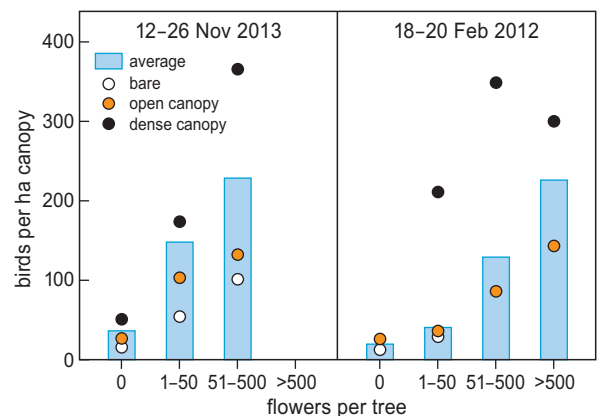
Figure 18. Birds per ha canopy for *Acacia seyal* in a floodplain in the Inner Niger Delta (Mali) in November (1033 trees; left) and February (447 trees; right) as a function of the number of flowers in a tree (bars). The flowers were counted on one side of the tree only, so actual numbers must be twice as high; most trees were 5 m high and 6 m wide. The same data are given separately for trees for which opacity differed (three categories, dots); statistical details in endnote[xxi].

50 flowers (Figure 18). The variation in bird density was particularly large in *Acacia seyal* because the opacity varied so much locally and temporally, again making clear that opacity should be scored when counting birds in trees.

Another, as yet unmentioned, variable that may explain bird density is the presence of climbers which may convert an unattractive tree into an attractive one when its semi-parasite carries berries or flowers (Stoate 1998). Sunbirds never visited *Vitellaria paradoxa*, for example, unless this tree species was adorned with the semi-parasite *Tapinanthus* spp. in flower (*n* = 6).

Flocking and interference competition

So far, bird density in trees has been related to various micro-habitat variables, but part of the variation in bird density might be due to the tendency of birds to feed in flocks. In fact, 98.6% of all shrubs and trees were found to be devoid of birds. The other extreme was represented by a single, large *Faidherbia* with 17 birds of seven species. However, trees with birds usually held just a single individual per species. Even in large *Faidherbia*, 89% of the Olivaceous Warblers and 85% of the Subalpine Warblers were single. The three *Sylvia* species and Olivaceous Warbler were probably territorial as evident from the aggressive encounters with conspecifics and other birds. As a consequence, on the rare occasion that more than one individual of these species occurred in a tree, it often did not last long before one of the birds was chased away from the tree. *Phylloscopus* species were more tolerant, but even in large *Faidherbia* still 44% of the Bonelli's Warblers were alone.

We recorded Olivaceous Warblers chasing eight insectivorous bird species, apart from conspecifics. Subalpine Warblers were often aggressive, although less frequently than recorded in Olivaceous Warblers, towards the (smaller) *Phylloscopus* species. Aggression occurred so often, that we became convinced during the field work (as were Salewski *et al.* 2007) that the density of *Phylloscopus* species, although related to the habitat variables as shown above, must have been reduced in the presence of Olivaceous and Subalpine Warblers. The statistical analyses, however, did not support the impression that interspecific aggression prevented some species from using trees occupied by a dominant bird species. On the contrary, all bird species tended to select tall trees with a dense canopy or flowering (Figures 14, 15 and 18). But perhaps the impact of interference competition was masked by tree quality? To check this possibility, we reanalysed the data in Figure 15 for Bonelli's Warbler and for the

Phylloscopus species combined and used the density of Olivaceous and Subalpine Warbler as additional variables in the analysis. In all cases, the presence of the dominant bird species had no significant negative effect on the density of subordinate species [xxi].

DISCUSSION

Detection probability

No matter how talented an observer, or how sophisticated and standardised the sampling techniques, variable detection probabilities remain problematic in those birds living a secretive life, as do woodland birds. Youthful confidence in one's own prowess in producing reliable censuses, is over the years replaced by doubt. Many studies using relative census methods do not even come close to reality, and appear not to be aware of the problems surrounding variable detection probabilities (in this regard, the overwhelming use of indices of abundance in bird census work is worrying; Rosenstock *et al.* 2002, Anderson 2003). A revealing example of the problems involved is provided by Bächler & Liechti (2007), who reviewed the detection probability in studies on bird densities. They had to conclude that none of the studies quantified detectability and half of the studies did not even mention it. Apparently, the implicit assumption is that the detection probability is invariable and thus index counts can be converted directly into absolute densities. From their own work, Bächler & Liechti (2007) provided a dramatic example that there is no reason to assume this to be correct. They radio-tagged nine Orphean Warblers in an oasis in Mauritania and tried to locate these birds in the following days, once in the morning, once at noon and once in the evening. The radio-tagged birds were relocated 264 times, but visual detection was successful only in 59% of the relocated birds (with the bird's position exactly known from the tag's signal), spending 5 minutes of searching for each radio-located bird by a single observer. Searching for a bird in a tree during 5 minutes is a long time compared to standard bird counts, but clearly did not suffice in many cases. It is another reminder that counting birds, and especially obtaining reliable absolute numbers, is very difficult indeed (a problem not solved by using methods that produce relative bird numbers; see for example Manu & Cresswell 2007).

The above-mentioned case of Orphean Warblers to a large extent fits our experience with obtaining absolute bird numbers. Among the 51 bird species covered by our survey, Orphean Warbler was the most

difficult bird to detect in the woody vegetation in the Sahel (Figures 6A and 6B). We may therefore assume that the detection probability of Orphean Warblers is lower than for more mobile foliage-gleaners. Locating birds in a tree may improve when using two or three observers, rather than one (as in the study of Bächler & Liechti 2007), who can cover the canopy from various angles and keep each other informed on movements and sounds. Also, finding birds in *Acacia tortilis* or *Balanites aegyptiaca*, the tree species used by the Mauritanian Orphean Warblers (Bächler & Liechti 2007) is typically difficult and time-consuming because of their dense canopy (Figure 4). For large trees such as *A. tortilis* we spent an observation time of 2–8 minutes with two observers (Figure 4), i.e. a much larger effort than in the Mauritanian oasis (Bächler & Liechti 2007). How many Orphean Warblers we would have overlooked if our observation time had been halved is difficult to say. Figure 8 suggests that 31% of Common Whitethroats and 23% of Subalpine Warblers would have escaped detection. Compared to these *Sylvia* species, the Orphean Warbler is still more difficult to detect, so it is conceivable that a failure to locate 41% of the Orphean Warblers, as in the study of Bächler & Liechti (2007), is entirely within the range of non-detection if our observation time had been reduced by half.

To complicate matters, the Orphean Warblers studied by Bächler & Liechti (2007) might have been more difficult to detect than their congeners in our sampling plots. Their study was performed in late April when the local temperature varied between 28°C (21–41) at sunrise and 40°C (37–45) at noon (temperatures taken from the nearby airport of Atar). With such extreme temperatures more birds may have been forced to remain inactive in the shadow for part of the day (as shown by Tieleman *et al.* 2003, Martin *et al.* 2015), thus being more difficult to detect. If so, one would expect that the detection probability would have been high in the morning and low at noon. In contrast, our data were collected between early October and mid-March, when on average the temperature during daylight varied between 13 and 41°C. Temperatures of >40°C become more frequent from mid-February onwards when the average temperature gradually increases by 5°C until April, but were still rare during the periods of our fieldwork. At the time we overlooked three birds during our experiments with detection probabilities (Table 1), conditions were exceptional with very high temperatures, resembling those in Mauritania (Bächler & Liechti 2007). However, conditions during our fieldwork were usually more benign and the

analyses to investigate whether observed bird density was lower at higher temperatures showed contrasting results without a clear pattern, suggesting that only very high temperatures induce inactivity [xxii].

Of all variables potentially influencing detection probabilities, secretive behaviour and temperature are but two of many. Our study shows that, in the setting of Sahel and adjoining vegetation zones where trees are scattered and most birds are recorded visually rather than by ear (Figure 11), detection probabilities varied substantially with tree properties such as canopy surface (Figure 4), canopy volume (Figure 5A) and opacity score (Figure 5C), and with species-specific bird behaviour (Figure 8, 9, 12, 13). Absolute bird densities, at least when validated, have the advantage that confounding variables such as detection probabilities, are effectively nullified. But it comes with a cost: time.

Measuring absolute bird density per tree: no compromises

Our census method is time-consuming. To count the birds in a tree 10 m wide, two observers spent 1.4 s/m² canopy for a tree such as *A. seyal* with rather low opacity (hence 'easy'), but 3.6 s/m² for a *Faidherbia albida* (Figure 4). This translates into an effort of 4–10 h for two observers to count all the birds in one ha of forest with only *A. seyal* and *Faidherbia*, assuming that the woody cover would be 100%. The time we actually spent per ha was much lower because the woody cover in most of our 1.5 ha-plots varied between 1 and 10%. Also, shrubs took us much less time than trees. On average, counting birds in trees and shrubs on one ha of Sahelian wooded savanna or cropland took three persons 16 min, on average, but this varied between 1 and 242 min/ha depending on local conditions.

Given the variable detection probabilities any compromise to reduce observation time should be avoided. To improve detection, using playback might be an option. In the mangroves of West Africa, we used playback song of Palearctic bird species to try to find undetected birds, but to no avail (Zwarts *et al.* 2014). A better strategy might have been to play alarm calls. However, alarm calls directed at owls or snakes tended to attract birds from all over the place, resulting in a mob of birds whose origins were mostly unknown (from which trees, from outside the plot or not?). We therefore refrained from using playback in Sahelian woodlands, although it might perhaps be used for isolated trees or impenetrable thorny shrubs.

Counting birds in separate trees is not difficult when they are standing apart, but is the method also feasible in forest? After all, birds in a forest move more

Figure 19. *Faidherbia* on farmland near M'Bour, Senegal, on 26 January 2014. The trees on the left photograph have been heavily pruned in the previous dry season. These trees were unable to produce much foliage in the following wet season, and no flowers at all (hence no pods later on). The right photograph shows one of the ten relatively untouched *Faidherbia* trees at the same site with a dense crown (i.e. high opacity, large relative canopy volume); each of these trees contained 2000–4000 flowers or 2000–5000 pods. Birds were absent in the trees on the left picture, but 2–8 birds resided in the ten untouched trees.

easily between trees compared to those occupying trees in an open savanna where they have to cross open spaces to access another tree. When woodland was dense, we opted for an alternative, but still fully quantified, method. Whilst one of us recorded all trees within the plot, noting all variables as routinely done for separate trees, the other observers carefully searched all trees within the plot for birds. Any birds found were passed on to the note-taker with details of the specific tree. Combining both data sets yielded the same information as when separate trees were checked in farmland or open savanna. Several problems arise, however, if the forest is dense and individual tree canopies overlap, for example regarding roaming birds (Granholm 1983) and measuring tree heights with a laser rangefinder. Therefore, our method of censusing birds is probably less suited to temperate and tropical forests, although it may be feasible for solitary trees, hedgerows and woodlots in farmland.

Relevance of measuring bird density per tree

Our data illustrate the large temporal and spatial variation in tree condition, related to species and size (Figure 14), volume and opacity (Figure 15A), open patches in canopy (Figure 15B), berries (Figure 17) and flowers (Figure 18). Each of these variables contributed

to the tree's suitability as a foraging site for birds and some of these variables show consistent variations relative to season (Figure 18) or rainfall. Birds will find more food in trees with more leaves, flowers or eatable berries, but why are there so remarkably few birds in trees with an open crown (Figure 15B): is it simply less food, or perhaps lack of cover (Martin *et al.* 2015)? Due to pruning, the shape and density of the crown is highly variable in Sahelian trees (Figure 19). In the Sahel trees have an important economic function, especially as firewood and food for livestock. Branches, twigs, flowers and pods are cut or clipped to feed livestock during the dry months. Consequently, trees with a well-developed canopy have become rare. Clipping also explains why canopy volume of trees relative to tree cylinder volume varied so much in a heavily pruned species such as *Faidherbia*. Human-caused variability in tree properties makes it all the more important to systematically collect data per individual tree in order to understand changes in bird numbers across regions, seasons and years.

Most likely, birds track seasonal changes in leafing, fruiting and flowering (Jordano 1988, McGrath *et al.* 2008; see also Figure 18), but to what extent and significance for survival is still unknown. The phenology of leafing, and also the amount of leaves produced by

Sahelian trees, are known to differ annually depending on rainfall (Poupon 1979). In extremely dry years, trees produce few leaves and the survival prospects of migratory tree-dwelling birds must then be poor indeed, as evident from steep population declines under such conditions (Zwarts *et al.* 2009). Nevertheless, although the phenology of Sahelian tree species, insects and birds have been described in a number of cases (e.g. Morel 1968, Gillon & Gillon 1973, Poupon 1979, Depommier 1998), the link between tree phenology, insect phenology and Palearctic birds has not been quantified (but see Salewski *et al.* 2006). We need more tree-specific data to unravel the causal pathways that connect local tree condition, bird numbers and bird survival.

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SAMENVATTING

Voor een onderzoek naar de verspreiding, talrijkheid en habitat-keuze van Palearctische bosvogels die ten zuiden van de Sahara overwinteren, hebben we een telmethode ontwikkeld die gericht is op het verkrijgen van absolute dichtheden. In ruim 2000 plots (elk 300 × 50 m groot) willekeurig verspreid over West-Afrika werden in de droge tijd (oktober–maart 2007–2015) alle aanwezige bomen op naam gebracht (183 soorten) en opgemeten door dezelfde waarnemer. Elke boom werd tege-lijkertijd door twee andere waarnemers net zo lang bekeken totdat zeker was of er al dan niet vogels in zaten. De tijdsduur voor het bekijken van één boom of struik varieerde van 1 tot 2502 sec., overeenkomend met respectievelijk een kaal boompje en een dicht bebladerde reus. De observatietijd nam toe met het aantal vogels in de boom. De meeste vogels werden aan het begin van de observatieperiode opgemerkt. Ongeacht de aanwezigheid en het aantal vogels in de boom werd gemiddeld nog ongeveer 300 sec. waargenomen nadat de laatste vogel (of geen vogel) was gemeld (de opgeeftijd). Van de aanwezige vogels werden aantal en identiteit vastgesteld (soms aangevuld met gegevens over geslacht en leeftijd), zo ook het gedrag (stil of roepend, foeragerend of inactief, hoogte in de boom of struik, interacties, soms vluchtafstand en foerageerwijze). In totaal hebben we op deze manier ruim 307.000 bomen bekeken. Slechts 1,4% van deze steekproef bevatte één of meer insecti-vore vogels (de lokale zaadeters bleven buiten beschouwing), de rest was leeg. De verkregen vogeldichtheid hebben we op verschillende manieren proberen te valideren. Omdat we de hele dag door vogels hebben geteld (van vlak na tot vlak voor burgerlijke schemering), zijn we nagegaan of de dichtheden afnemen in de loop van de dag, een fenomeen dat op het noor-delijk halfrond zo uitgesproken is dat daar inventariseren na het middaguur wordt afgeraden. Dat bleek niet het geval, of althans niet duidelijk. Vermoedelijk komt dat doordat het overgrote deel van de vogels in de Sahel op zicht wordt gevonden, niet op gehoor (een wezenlijk verschil met inventarisaties in de gema-tigde klimaatzone), en de hele dag door actief foerageert. Bij 321 dichtere bomen toetsten we bovendien of we vogels hadden gemist tijdens de normale observatieperiode door de bomen na de opgeeftijd te bekogelen met stenen, takken en koeienpoep. Van de 57 waargenomen vogels bleken we er 3 te hebben gemist, telkens bij zeer hoge temperaturen. Omdat bomen met een dichte kruin minder dan 10% van het totaal uitmaken (bij een willekeurige steekproef), zeer hoge temperaturen vooral pas na half maart standaard zijn (buiten onze waarneemperiode) en vogels in de Sahel zelden inactief zijn, durven we met enige zekerheid te zeggen dat onze absolute telmethode betrouwbare gegevens heeft opgeleverd.

ENDNOTES

[i] Canopy width (*W*) as measured in the field and on the photographs (both determined as fraction of tree height (*H*)) were highly correlated: $W_{photo} = 0.866 \times W_{field} + 0.32$ ($r^2 = 0.91$; $n = 795$, $P < 0.001$; range of width: 5–35 m). The width was slightly underestimated in slender trees ($H > W$) and overestimated in relative wide trees ($W > H$). To correct for this, all field estimates of width were adjusted: canopy width = –0.546 ($\pm$ 0.187) + 0.798 × W_{field} ($\pm$ 0.013) + 0.164 × H ($\pm$ 0.023); (SE between brackets, $r^2 =$ 0.91, $n = 795$, $P < 0.001$).

[ii] High-resolution satellite images clearly show that Sahelian trees have a circular canopy, although due to pruning the form of old trees may become irregular. Since *Faidherbia* are pruned so often, their canopies deviate more often from circular than other tree species. In 17 *Faidherbia* trees photographed from 2–4 sides, width measurements deviated, on average, by 6% from the average width. The deviation was 7.7% in 28 *Faidherbia* trees where width was estimated in the field from different positions.

[iii] Number of birds observed and total duration of observations in seconds (including minimum, maximum and median durations) used to describe foraging behaviour in trees in the Sahel and the Sudan vegetation zone.

Species	number	s	min.	max.	median
Orphean Warbler	13	339	9	61	21
Subalpine Warbler	36	1135	8	170	23
Olivaceous Warbler	24	1059	12	213	25
Common Whitethroat	14	523	14	94	27
Eur. Pied Flycatcher	120	17185	16	660	116
Bonelli's Warbler	88	3103	9	151	29
Willow Warbler	10	471	17	60	46
Wood Warbler	9	1014	13	371	76
Common Redstart	20	5550	11	3720	23

[iv] The observation time is known for 1636 *Faidherbia*, 684 *A. seyal*, 206 *A. tortilis* and 150 *Balanites*. Figure 2 gives the average value per category, based on a variable number of measurements: 42–176 in *Faidherbia*, 5–159 in *A. seyal*, 7–33 in *A. tortilis*, and 14–40 in *Balanites*. The sample is smallest for the taller trees; hence these categories were lumped (e.g. 16 + 17 m and 18 + 19 + 20 m in *Faidherbia*). The SE as % of the mean amounted to 8%, on average, in *Faidherbia*, 14% in *A. seyal*, 18% in *A. tortilis* and 20% in *Balanites*. A univariate analysis of variance (four tree species and canopy width per m; 14 classes) was performed on the raw data to test whether the observation time differed for the four tree species. Canopy width and the four species differed significantly ($P < 0.001$); the interaction term was not significant ($P = 0.259$), total $r^2 =$ 0.503, $P < 0.001$, $n = 2676$.

[v] Figure 3 gives the average observation time per category, based on a variable number of measurements: 12–158 for canopy volume, 9–697 for canopy cylinder volume, 14–763 for number of birds and 45–784 for opacity; SE is indicated if visible. A multiple regression analysis, performed on the raw data, revealed that in *Faidherbia*, canopy volume$^{0.5}$ ($P < 0.001$), number of birds ($P < 0.001$) and opacity ($P = 0.001$) all significantly contributed to the explained variance, in total 62% ($n = 429$, $P < 0.001$). The broken lines in Figure 3B and 3C refer to unstandardized regression coefficients from this multiple regression analysis. The explained variance still amounted to 58% when in the same analysis tree cylinder$^{0.5}$ instead of canopy volume$^{0.5}$ was used as a proxy for tree size; all three variables were highly significant ($P < 0.001$; $n = 1159$, $P < 0.001$).

[vi] We did an analysis of covariance to analyse the observation time for 2676 trees for which we measured canopy surface, tree height and number of birds as covariate and tree species ($k = 4$), opacity ($k = 5$) month ($k = 4$) and year ($k = 3$) as factors (k = number of classes); there were no missing values. All variables were significant ($P < 0.001$). Canopy surface was dominant with $r^2 = 0.409$ for this variable alone. For tree height alone $r^2 = 0.302$. Since both variables were highly correlated, r^2 increased only by 0.018 to 0.427 when both variables were included in the model. $r^2 = 0.425$ for number of birds as single variable, but this was reduced to $r^2 = 0.156$ when entered in the model after both tree dimensions. For opacity as a single variable $r^2 = 0.209$, but r^2 was reduced to 0.056 when entered successively into the model. r^2 as a single or added variable amounted to, respectively, 0.189 and 0.004 for tree species, 0.110 and 0.004 for month and 0.091 and 0.014 for year. Hence tree canopy, number of birds and opacity explained 63.1% of the variance; the four other variables added not more than 3.5% to the explained variance. The difference in observation time between tree height, tree species, months and year mostly disappeared after taking into account the other variables.

[vii] Giving-up time, measured in 1097 *Faidherbia* trees, was, according to a multiple regression analysis, related to canopy surface ($r^2 = 0.23$, $P < 0.001$) but not to the number of birds ($P = 0.026$; the total explained variance increased with a meagre 0.4% when number of birds was added to the analysis). When opacity was included in the analysis, the total explained variance increased significantly to 47.9%, of which 0.0% by number of birds present.

[viii] SE was small (on average 20 s, varying between 8 and 46 s) and is not indicated. SE as % of the mean amounted to 5% in 0 and 1 bird, 9% in 2 birds, 11% in 3 birds and 12% in 4 birds.

[ix] The activity was known for 1059 Bonelli's Warblers and 553 Subalpine Warblers. We performed linear regression analyses on the percent inactive birds averaged per degree Celsius varying between 14 and 40°C. There were more inactive birds at higher temperature, but the trends were not significant in Bonelli's Warbler ($r^2 = 0.09$, $n = 27$, $P = 0.06$) and in Subalpine Warbler ($r^2 = 0.10$, $n = 27$, $P = 0.07$). A logistic regression analysis on the raw data gave the same results: no significant trends for Bonelli's Warbler ($P = 0.260$) and Subalpine warbler ($P = 0.216$).

[x] According to logistic regression analyses, the seasonal variation in feeding activity was non-significant in Bonelli's Warbler ($P = 0.061$; $n = 1082$), Subalpine Warbler ($P = 0.109$; $n = 577$), Olivaceous Warbler ($P = 0.655$; $n = 366$) and Common Whitethroat ($P = 0.304$; $n = 128$).

[xi] According to logistic regression analyses, the variation in feeding activity during the day was significant in Bonelli's Warbler ($P = 0.001$; $n = 1082$; higher activity in early morning and late afternoon than around noon), but not significant in other species: Subalpine Warbler ($P = 0.139$; $n = 577$), Olivaceous Warbler ($P = 0.569$; $n = 366$) and Common Whitethroat ($P = 0.295$; $n = 128$).

[xii] Vocal activity was noted for 588 Subalpine and 1082 Bonelli's Warblers and averaged per hour relative to civil twilight in morning and evening. The average activity was calculated per h (shown in the graphs). The regression lines, referring to these 12 averages and only shown when significant, were linear but since the relationships shown in A and B (only 'quiet') were curved, a second degree polynomial was fitted four times.

[xiii] We analysed, separately for the four tree species and the seven most common bird species, whether bird density (n/ha canopy) varied during the course of the day. To rule out the variation due to all other variables, we calculated per tree species the average density for the 12 daylight hours (hour relative to twilight in morning and evening). A second-degree polynomial was used to test whether the measured, average density was lower at noon than in the morning or late afternoon. This was the case in 14 analyses (of which 3× significant, $P < 0.01$: Common Whitethroat in *Faidherbia*; Orphean Warbler in *A. tortilis* and (Iberian) Chiffchaff in *Balanites*). The opposite was found in the 14 other analyses (of which one was significant: Olivaceous Warbler in *Faidherbia*). A linear regression was calculated to test whether the measured density declined for the 12 daylight hours. A decline was found in 17 analyses (of which 1 significant: Common Whitethroat in *Faidherbia*) and an increase in 11 analyses (none significant). These results cannot be interpreted as an indication that we overlooked more birds in the middle of the day or an increasing fraction during the course of the day.

[xiv] We calculated per bird species whether the fraction of birds detected by eye or by ear varied between the four tree species which can be ranked according to the opacity of the canopy from open to dense: *A. seyal*, *Faidherbia*, *A. tortilis* and *Balanites*. In Bonelli's Warblers, the fraction recorded by eye indeed declined (85, 86, 76, 72 % by eye, respectively), but there was no clear trend in Subalpine Warblers (72, 76, 55, 64%) and no trend at all in the five other most common bird species.

[xv] We did a stepwise multiple regression analysis to investigate how number of birds per tree was related to canopy surface and tree height. To rule out the variation due to variables such as opacity and get a normal distribution, we calculated the average number of birds per tree height (per m) separately for trees varying in canopy surface (canopy width per m); we left out cell values based on less than 10 trees. In *Faidherbia* ($n = 84$), r^2 for canopy surface was 0.772 ($P < 0.001$), the contribution of tree height to the explained variance was small (added $r^2 = 0.006$, $P = 0.355$). Also in 3 other tree species we found that bird number was related to canopy surface and that tree height added nothing (*A. seyal* and *Balanites*) or not much (*A. tortilis*) to the explained variance:
A. seyal ($n = 44$) surface ($r^2 = 0.566$, $P < 0.001$) and height ($r^2 = 0.009$, $P = 0.350$);
A. tortilis ($n = 41$) surface ($r^2 = 0.694$, $P < 0.001$) and height ($r^2 = 0.098$, $P < 0.001$);
Balanites ($n = 40$) surface ($r^2 = 0.722$, $P < 0.001$) and height ($r^2 = 0.006$, $P = 0.355$).
The fact that height is statistically not significant (due to the high correlation between tree height and canopy surface; see Figure 2A) if we know the canopy surface, does not imply that tree height is less relevant biologically.

[xvi] The average number of birds per category (canopy width in m) was calculated by dividing number of birds counted (summated per category) by total canopy surface (summated per category). Hence

no SE can be indicated. The linear regression lines, referring to the 11–22 average values, were highly significant ($P < 0.001$). Explained variance (r^2) and total number of trees in which birds were counted amounted to 0.983 and 4866 in *Faidherbia*, 0.959 and 16,990 in *A. seyal*, 0.964 and 14,621 in *A. tortilis* and 0.987 and 19,380 in *Balanites*, respectively. r^2 (given in the graph) declines in *Faidherbia* to 0.92 if a power function is fitted (exponent 1.2) from which we may conclude that a linear regression gives the best fit. In the other three species r^2 hardly changed at a power function (exponents 1.2 in *Balanites*, 1.3 in *A. tortilis* and 1.4 in *A. seyal*). From this we conclude that the relationships hardly deviated from linearity, but also that birds reach a higher density in trees with a larger canopy surface.

[xvii] In *Faidherbia* trees with 0, 1–10, 11–100, 101–1000 and >1000 flowers (flowers visible from a distance, counted on one side of the canopy), we counted 87±5, 108±19, 133±18, 165±13 and 325±59 birds ± SE/ha canopy, respectively ($n = 1025$, 78, 216, 289 and 82). Since *Faidherbia* with flowers usually also have a dense foliage, we did a two-way analysis of variance on bird density per ha as a function of opacity and numbers of flowers (both 5 classes): $P < 0.001$ for flowers, $P = 0.014$ for opacity; $P = 0.014$ for the interaction term; total: $r^2 = 0.099$; $P < 0.001$, $n = 1690$. Concluding: flowers and opacity have a highly significant impact on bird density, but the unexplained variance is large.

[xviii] The regression lines in Figure 15A were highly significant ($P = 0.001$); a logistic regression analysis on the raw data (presence of birds as a function of canopy surface and opacity; $n = 1786$) gave the same significant result (Nagelkerke's pseudo-$r^2 = 0.291$). A one-way analysis of variance of the data given in Figure 15B revealed that opacity and relative canopy volume were highly significant factors ($P < 0.001$); also the interaction was highly significant ($P < 0.001$). However, it should be noted that the summed explained variance was only 10% ($n = 450$); a logistic regression analysis (presence of birds as a function of canopy surface, opacity and relative canopy; $n = 450$) revealed that opacity was weakly significant ($P = 0.017$) and canopy surface and relative canopy volume highly significant ($P < 0.001$); Nagelkerke's pseudo-$r^2 = 0.320$.

[xix] We did 144 measurements, here taken together in 9 categories (n per category varying between 5 and 33). The regression lines were highly significant ($P < 0.001$). A second-degree polynomial was used to fit the curved relationship for all birds. If the regression lines were calculated for the 144 measurements, the trends were also significant for all birds ($r = +0.283$, $P = 0.003$) and for *Phylloscopus* ($r = +0.245$, $P = 0.005$).

[xx] We saw no birds in 961 of the 1138 *A. seyal* trees (84.4%) and 1, 2, .. 6 birds in 144, 21, 6, 3, 2 and 1 tree, respectively. A logistic regression analysis of the presence of birds per tree (0 or ≥ 1) with season as factor and canopy surface as covariate showed that both were highly significant ($P < 0.001$; Nagelkerke's pseudo-$r^2 = 0.089$. If opacity and presence of flowers (categories as in Figure 16) were added as factor, pseudo-r^2 increased to 0.222, with a significant contribution of both factors ($P < 0.001$), but the significance of season became less, although still significant ($P = 0.005$). A one-way analysis of variance (less reliable due to the skewed distribution) revealed a similar result: the bird density in *A. seyal* trees depended on opacity ($P < 0.001$) and density of flowers in a tree ($P < 0.001$, as well as on the interaction between both main effects ($P < 0.001$); also season was significant, but less so ($P = 0.012$). Total: $r^2 = 0.195$; $n = 1138$.

xxi The density per canopy surface of Bonelli's Warbler in *Faidherbia* trees was positively correlated to those of Subalpine Warbler and Olivaceous Warblers (although hardly significant, $P = 0.045$ and 0.053 respectively; $n = 3258$). In a multiple regression (density of Bonelli's Warbler as a function of opacity, number of flowers, presence of Olivaceous Warbler and Subalpine Warbler), the relation with both bird species became negative (as expected, assuming interspecific competition), but non-significant ($P = 0.273$ and 0.187, respectively). The analysis was also done with a logistic regression: presence of Bonelli's Warbler per tree (recoded to 0 and ≥1) as function of two factors (flowers and opacity), and three covariates (canopy surface, number of Olivaceous Warblers and Subalpine Warblers); all variables were highly significant, but the presence of Bonelli's Warbler was not related to the numbers of Olivaceous Warblers and Subalpine Warblers in a tree.

xxii We analysed, separately for four tree species and the seven most common bird species, whether bird density (n/ha canopy) was related to temperature (averaged per degree Celsius). In 8 multiple regression analyses we found an increase, of which one was significant ((Iberian) Chiffchaff in *A. tortilis*) and in 20 analyses a decline, of which one was significant (Bonelli's Warbler in *Faidherbia*). These results cannot be interpreted as an indication that high temperatures were conducive to overlooking birds.