Grasshopper country before and after: a resurvey of Ken Key's collecting expeditions in NSW, Australia 70 years on

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Abstract

Recent reports of insect declines across Europe and other parts of the world have emphasized the generally poor baseline that exists for assessing changes in biodiversity. One important source of untapped baseline distribution data are field notebooks, which are often associated with the collection activities of museums and other scientific institutions and may be decades or even centuries old. Over 220 field notebooks are associated with the grasshopper (Caelifera) collection in the Australian National Insect Collection, containing detailed notes on the times and places species were collected as well as vegetation and soil descriptions. In 2019, we resurveyed 45 locations from three of these notebooks from the 1940s, to assess the potential value of larger scale efforts in the future. We found substantial differences in grasshopper species richness and composition between the surveys; richness was generally higher in our survey and some species showed dramatic increases in range and occurrence whereas others remained relatively static. There was also evidence for vegetation state transitions in some areas, including increased weediness and shrub thickening, which may be associated with changes in the grasshopper fauna. We developed approaches for comparing environmental conditions across surveys and found that our species richness and abundance estimates were positively correlated with rainfall in the year preceding each survey. We conclude that further resurvey work on these field notebooks will provide a strong baseline picture of the diversity, distribution and abundance of the Australian grasshopper fauna for assessments of future change and may also give new insights about associated vegetation changes.

Keywords: grasshopper, resurvey, historical, field notebook, monitoring

Introduction

Long term perspectives are necessary for understanding ecological processes and trends including species decline. In entomology, for example, significant insect declines have only been detected with the aid of datasets spanning decades. These include the 75% decline detected over a 27 year period in flying insects in Germany (Hallmann *et al.* 2017), and in many other insect taxa in different parts of the world (Sánchez-Bayo and Wyckhuys 2019). The reviews of Sánchez-Bayo and Wyckhuys (2019, 2021) revealed strong biases in our understanding of insect decline both geographically (bias towards Europe and North America) and taxonomically (bias towards Hymenoptera and Lepidoptera). This bias makes it difficult to assess the relative importance of the different drivers of decline, and therefore to develop broad policies and management strategies to prevent further declines (Janzen and Hallwachs 2019).

Two particularly striking gaps in our understanding of insect decline apparent in Bayo and Wyckhuys's review (2019) are the lack of data on Orthoptera (one study of German crickets) and Australia (one analysis of introduced honeybee trends). Among the orthopteran insects, grasshoppers (Acrididae) are dominant invertebrate herbivores and a ubiquitous component of grassland ecosystems worldwide, contributing to more than half of the total arthropod biomass in the aboveground grass layer (Gillon 1983). They exert a significant ecological impact in grasslands in terms of nutrient cycling (Mitchell and Pfadt 1974; Belovsky and Slade 2002) and grazing (Andersen and Lonsdale 1990) and provide an important source of nutrition for invertebrates (Joern *et al.* 2006) and vertebrates (Gandar 1982), thus supporting other biological components of the ecosystem (Belovsky and Slade 1993). Furthermore, several grasshoppers and locusts can periodically outbreak and cause enormous economic damage to agriculture. Thus, the lack of data on grasshoppers is curious (but see Nufio *et al.*, 2010).

Australia is 'grasshopper country' (Rentz 1996), with well over 1000 orthopteran species known, >90% of which are endemic. They were studied extensively in the mid-1900s from a taxonomic and ecological perspective, motivated by a need to understand and control outbreaks and their agricultural effects (Andrewartha and Birch 1954; Key 1992), but they were also the subject of evolutionary and genetic studies because of their amenability to cytological analyses (White 1973). Their high taxonomic and ecological diversity, as well as their generally high abundance and ease of sampling, make them potentially valuable indicator species of general changes in climate and habitat, but they have not been used in this manner thus far.

Australia has relatively little published historical data on invertebrate populations generally, but there is scope to redress this issue by replicating past surveys (Rix *et al.* 2017; Braby 2019; Didham *et al.* 2020), an approach referred to as the ‘snapshot effect’ (Didham *et al.* 2020). One potentially rich source of historical information on insect distribution and abundance in Australia are the field notebooks of Ken H. L. Key and his associates. Between 1936 and 1989 Key and his colleagues undertook 223 systematic surveys across the road network spanning the Australian continent, surveying the grasshopper fauna approximately every 16 km (10 miles), resulting in ~2400 pages of notes covering ~2700 days of survey effort, adding ~130,000 pinned specimens of ~400 species to the CSIRO Australian National Insect Collection (ANIC) (You Ning Su, pers. comm.). Key and associates systematically recorded their field observations in those notebooks, providing collection locations, terrain type, general habitat descriptions, details on the plant species found and, of course, the species of grasshopper present, all of which are associated with physical specimens housed in the ANIC. These documents provide a valuable baseline of the grasshopper fauna that is likely to be sufficiently detailed to enable resurvey and meaningful comparison. Despite their potential value, most of the records from Key’s expeditions have not yet been incorporated into modern databases, and the detailed information in the notebooks remains unexplored.

This study aimed to undertake a preliminary resurvey of locations in New South Wales (NSW) surveyed by Key and his associate L. J. Chinnick in 1946, 1948 and 1949. We revisited 45 sites across agricultural lands and native vegetation and asked how the vegetation and grasshopper species diversity and composition varied from Key’s surveys over 70 years earlier. We had the following aims: (1) To check whether Key’s locations could be accurately re-located based on the notes and collect comparable information from 2019; (2) To assess whether the difficulties in interpretation (biases, detection, qualitative nature of some original data, imprecise locations) can be overcome such that useful comparisons can be drawn (and if so, whether further re-sampling is warranted); (3) To compare the grasshopper faunas from the 1940s and 2019 (~75 years) and to form hypotheses for the causes of any apparent changes to guide further targeted research.

Materials and Methods

Overview of Approach

We attempted to replicate the sampling methodology and locations used by Key and colleagues that were originally visited during 28-29 October 1946 (14 sites, field notebook number 16), 29 November–1 December 1948 (24 sites, field notebook number 20) and 21 October 1949 (7 sites, field notebook number 22). These sites span a strong east-west rainfall gradient from temperate grassland in the southeast to semiarid shrublands in the west, with a north-south rainfall seasonality and temperature gradient from cool with winter rainfall in the south to warm with aseasonal rainfall in the north (Fig. 1).

Historical resurveys can be limited by factors such as observer differences (detectability) and location errors (Kapfer *et al.* 2017; Verheyen *et al.* 2018; Didham *et al.* 2020). We acknowledge several factors limiting the inferences which can be drawn from this comparison, including:

- The influence of the weather preceding both the 1940s and 2019 surveys, which may overwhelm any long-term trends in the data even though both surveys were conducted in similar seasons (October-November-December) of the year;
- The low spatial precision of the 1940s observations (i.e. lack of exact spatial coordinates), such that we cannot be sure whether our locations match them;
- The lack of survey protocols from the 1940s, which prevented us from exactly replicating the earlier methods. This includes the potential differences in sampling effort between our 4-person team and the unknown number of people surveying in the 1940s (likely 1–2 individuals). It also includes the varying expertise of participants;

- The stochastic nature of detection, such that at any given site a varying subset of the species present will be detected on any given survey event; the 1940s data did not employ a strategy of sampling / replication to deal with this stochastic variation.

We sampled in a manner designed to minimise, but not eliminate, these effects. To assess the role of recent weather conditions on our observations, we also quantified the short- and long-term environmental conditions during our survey and during the historical surveys (conducted in 1940s) using new mechanistic niche and microclimate modelling tools (Kearney and Porter 2020, 2017) (see 'Environmental Descriptions and Calculations', below). We also recorded the degree of confidence we had in the relocation of each site (see 'Vegetation Descriptions', below).

Grasshopper Sampling

Key's locations are specified by an odometer reading representing the distance by road from a reference point, given to the nearest mile (1.6 km), or more rarely to the nearest tenth mile (0.16 km). We used our own odometer, coupled with a pre-calculated place marker on Google Maps, to find candidate locations. We then used the original 1940s site descriptions of terrain and vegetation to find the most similar site within 1 km of the candidate location. For each of the resurvey sites, we obtained a geographic coordinate using Garmin GPSmap 60CSx.

At each location, in the 1940s, Key searched for grasshoppers for 30 mins (Day and Rentz 2004; Murray Upton pers. comm. 2019), while the search time for Chinnick is unrecorded but is probably also 30 minutes, given Chinnick was under Key's instruction. We do not know how many people were present during the 1940s surveys, but it was probably 1–2. For our 2019 surveys, three entomologists searched for grasshoppers for 30 mins, using visual inspection of the ground and shrub layers, along with a sweep net and bush-beating/shaking. The grasshopper samples were collected in 50 mL plastic vials, and were identified each evening at least to a genus level using Rentz et al. (2003). One botanist (SJS) collected site information for approximately 10 minutes, then assisted with grasshopper searches (but not identification). The relative years of experience of the grasshopper surveying team was: HS (20 years), MRK (15 years), AH (2 years), SS (0 years, 20 years botany). We are unsure whether all 'zero grasshopper' sites were recorded by Key and colleagues, although there are some such sites that include habitat descriptions. No samples were made after dark by us nor by Key and Chinnick.

At each location, we searched within a radius of approximately 100 metres, regardless of the degree of heterogeneity within this area. Our searches were confined to the areas we could access, often only the linear roadside verges. The 1940s site descriptions reveal that Key and Chinnick also sampled heterogeneous areas, but they did not report the area searched. Overall, we believe that this sampling methodology is consistent with Key's likely approach but acknowledge that our search effort is almost certainly greater than the 1940s surveys.

For each site we made an estimate of abundance (something Key and colleagues gave no indication of) using an arbitrary 8-point semi-quantitative scale (0,0.5,1,…3.5) agreed between all observers, using the following clear reference points: 0 = 'no grasshoppers present' (although we always found grasshoppers and did not use this category), 1 = 'low abundance' (total of < 5 individual grasshoppers per person observed over the 0.5 h), 2 = 'medium abundance' (grasshoppers regularly encountered every 1 minute or so) and 3 = 'high abundance' (grasshoppers almost constantly observable as the site was traversed), 3.5 'minor outbreak' (many grasshoppers constantly observable). The final estimate was agreed upon by the group at the conclusion of each survey.

Vegetation Descriptions

At every sampling location, we attempted to replicate the site information recorded by Key or Chinnick, and to provide additional useful information. The information recorded by Key and Chinnick was expressive, but did not follow a consistent pattern, with some elements omitted from some sites. In all cases they described the vegetation using general terms such as “savannah” and “dry sclerophyll forest”, and listed some common plant species (usually 1–5), although it is not clear whether these were the most abundant species, or if they were simply informative species with respect to grasshopper habitat. At most sites they described the height of the grass sward. Sometimes they made notes on the context or terrain of the site and occasionally they mentioned management issues such as overgrazing or soil scalds (relevant to oviposition sites). We collected the following information at each site:

- A checklist of whether each species or habitat element listed in the 1940s description remained present;
- A list of the common species at each site;
- An estimate of the percentage cover, across the surveyed area, of several groups of plants or habitat elements deemed of prominence in the local vegetation and of potential importance to grasshopper ecology. These were: *Eucalyptus*, *Acacia*, Casuarinaceae, *Callitris*, All other shrubs (not in the groups above), Cyperaceae, Poaceae, Asteraceae, Chenopodiaceae, All other forbs (not in the groups above), exposed ground (including rock and lichen), and leaf litter and debris. For each plant group, if relevant, we distinguished cover provided by native and exotic plant species;
- A judgement of the degree of grass sward greenness and maturity: 1 = green, lush and actively growing, 2 = in seed, ‘browning off’ or beginning to cure, 3 = cured, with most material turned straw-coloured and seeds released;

- A judgement of the extent to which the vegetation had changed since the 1940s. This assessment considered relatively stable factors such as tree and shrub density, grass cover, weed invasion and soil disturbance. It did not include shorter term changes caused by recent rainfall or recent grazing or mowing. The judgement was recorded as ‘negligible’ (no evidence for or reason to suspect substantial changes), ‘minor increase/decrease of some vegetation group’, and ‘major increase/decrease’ in some vegetation group;
- The confidence of site re-location was recorded in the following categories: ‘certain’ (clearly the same site, generally identified by distinctive features mentioned in the original accounts such as road junctions or named creeks); ‘high’ (within matching homogeneous area, sites which matched the habitat description, but no distinctive site details allowed the exact site to be determined), ‘medium’ (insufficient information to confirm, no reason to suspect an error, but not enough habitat information to confirm); or ‘low’ (suspected re-location error, could not reconcile the odometer reading with the habitat description).

Environmental Descriptions and Calculations

At the start of each survey we measured the air temperature at 1.2 m height in the shade using a 24-gauge Type T thermocouple thermometer (Fluke 52-II). Bare ground temperature in full sun, and ground temperature in the shade were measured with an infrared thermometer (ThermaTwin TN410LCE). A 25 mm copper tube painted brown with a thermocouple thermometer inside was placed on the bare ground patch in the sun for 5 mins and was used to estimate the operative temperature (Bakken and Angilletta 2014) of a grasshopper.

To compare the environmental conditions between our survey and the historical surveys, we used the mechanistic niche modelling package NicheMapR (Kearney & Porter, 2017, 2020) to compute metrics relating to short-term thermal conditions affecting grasshopper activity and longer-term estimates of food availability. Specifically, for each site we simulated hourly microclimates over a 10 year period leading up to the survey, following the approach of Kearney and Maino (2018) using the Australian Water Availability Project (AWAP) 5 km resolution grids (Jones *et al.* 2009) as weather forcing data and using the SoilGrids (Hengl *et al.* 2017) soil database for soil hydraulic properties. All default settings were used for the microclimate model. Unlike in Kearney and Maino (2018), daily windspeed data were unavailable for the years considered. The AWAP rainfall and air temperature (min/max) observations span the time period considered but vapour pressure and solar radiation do not (earliest data 1971 and 1990, respectively). Thus, we used simple linear regression (glm function of base R) models to estimate historical vapour pressure and solar radiation from rainfall and air temperature for a given site based on the relationship between these variables from 1990 to 2014 (rainfall, min/max air temperature and day of year used as variables for vapour pressure and radiation, with estimated clear sky solar radiation also used for solar radiation).

From the microclimate calculations we estimated a set of metrics relating to plant growth using the ‘plantgrow’ function of NicheMapR. This function takes as input the soil water potential calculations from the microclimate model at a specified depth range and a user-specified threshold soil water potential for the permanent wilting point to infer when a plant would be stressed and unable to grow. We used the default permanent wilting point value of -1500 J/kg (typical crop value; selected to represent a typical grass, the vegetation we assume is most relevant to a majority of grasshoppers) focusing on a depth of 25 mm with a 15 °C threshold for plant growth. We computed four increasingly sophisticated metrics of productivity over a period starting 30 days before a given survey and extending back one year: (1) the total rainfall, (2) the sum of hours of potential plant growth as determined by the threshold wilting point, (3) the sum of the percent hydration state of the vegetation (see Kearney *et al.*

2018 for details), and (4) the sum of a productivity measure that cumulates hours of plant growing degree days based on the wilting point threshold and a growth temperature threshold based on soil temperature.

Finally, we used the ectotherm model (Kearney and Porter 2020) to obtain estimates of the operative temperature of a non-thermoregulating grasshopper as well as the concurrent 1.2 m air temperature and ground temperature in the sun and shade.

Results

Site Relocation Success

During this study we revisited 45 historic survey locations from the 1946, 1948 and 1949 field notebooks (notebooks 16, 20 and 22, respectively) (Table 1, Fig. 1). Of these, 15 sites (33%) were classified as being relocated with ‘certain’ confidence, 24 sites (53%) with ‘high’ confidence, four sites (9%) with ‘medium’ confidence and only two (4%) with ‘low’ confidence (suspected re-location error). This high level of successful site relocation (86%) is promising for the prospects of using the notebooks as baseline data for further resurvey.

Species Richness

We recorded 43 species of grasshopper belonging to 32 genera, from across all 45 sites, compared to 39 species belonging to 27 genera in the 1940s. Only 19 species were common to both surveys (Table S1). Compared to the historic surveys, we recorded higher species richness from most of the sites we visited (30 of 45), the same number from 2 sites, and fewer species from 13 sites (Table 1, Fig. 2). In the 1940s surveys, zero grasshoppers were recorded from two sites (between Griffith and Hillston, Fig. 2) whereas we recorded 4–5 species from these sites during our re-survey. In contrast, the 1940s survey recorded

2–9 species from the most northern sites we sampled, between Nyngan and Bourke, compared to our 1–4 species (Fig. 2). The correlation in site richness between the surveys was not statistically significant and slightly negative (r = -0.24, P = 0.1163).

Species Occurrence

Of the more common genera we encountered, six showed a broadly similar distribution pattern in 2019 to the 1940s (*Praxibulus*, *Brachyexarna*, *Phaulacridium*, *Goniaea*, *Cryptobothrus*, *Chortoicetes*), whereas *Acrida*, *Macrotona*, *Peakesia* and *Oedaleus* were found substantially farther west in our survey than in the past, and *Peakesia* was also found farther south, while *Austroicetes* was noticeably absent in the north (Fig. 3). *Oedaleus* and *Goniaea* were found at many more sites in our survey but over a roughly similar spatial extent. More extreme was the case of *Acrida conica*, which was only recorded once in 1940s surveys (as a nymph) but in our 2019 re-survey this species was found at 19 sites (Fig. 3, Table 2), including adults from two sites, and often in high abundance. Similarly, only two locations yielded *Macrotona* species in the 1940s (one species per location). In contrast, we recorded four species from this genus from 27 locations (Fig. 3). *Macrotona* nymphs were present at high abundance at all sites that we observed the genus.

Vegetation

In comparison with vegetation observed in 1940s, we observed negligible or no changes for 16 sites, minor changes (i.e., weed invasion, grass layer declined and more shrub thickening, etc.) at 21 sites and major changes (i.e., site description is not matching with 1940s description, shrub thickening, more advanced weed invasion, exotic grass invasion, etc.) at eight sites (Table 1, Fig. 1b). Weed invasion was most pronounced in the wetter south east whereas shrub thickening was in the drier west and north

(Fig. 1b). Our more detailed quantifications of vegetation cover are provided in Table S1 and mapped in Figure S1.

Grasshopper Abundance (2019 only)

For 23 sites grasshopper abundance was found to be low (rank score 1-1.5), 19 sites as medium (rank score 2-2.5) and only three sites as highly abundant (i.e., grasshoppers constantly jumping over foot, rank score 3-3.5) (Fig. 4). At one site (notebook 20, 15022), *Austroicetes* and *Phaulacridium* were in a state of minor outbreak (rank score 3.5).

Environmental Conditions

Observations of thermal conditions during the 2019 observations were moderately well captured by the microclimate and ectotherm model simulations, with ground temperatures in the sun and shade matching best and 1.2 m air temperature having the poorest match (Fig. 5).

The biophysical model simulations suggested that the conditions during our survey were substantially hotter and drier than during the historical surveys (Fig. 6, paired t-tests all $P < 0.0001$).

Productivity measures were significantly correlated with our simple quantification of grasshopper abundance ($P < 0.0001$, Spearman Rank correlation), with all measures correlating with similar strength (Fig. 7). The productivity measures were also significantly correlated with grasshopper richness for our survey ($P \sim 0.01$, Pearson correlation) but not for the historical surveys (Fig. 8).

Discussion

Our knowledge of temporal changes in invertebrate biodiversity is generally limited and without strong baseline data. The field notebooks of Key and colleagues, representing over seven years of near-continuous field collection time, are a potential gold mine of information on the Australian Orthoptera and for the assessment of changes in their habitat and distribution. This paper serves as a pilot study to assess the potential value in large-scale resurveys of these and other notebooks in museums and herbaria. We aimed to determine the practicality of relocation and resurvey, to consider the potential biases of resurvey data and how they might be dealt with, and to draw some preliminary conclusions about how things have changed over the ~75-year time span between the two surveys. We discuss our findings under each of these aims.

Resurvey success

We were able to relocate 86% of the sites with high confidence. The recovery of locations via odometer records are necessarily limited in precision by the resolution of the original odometer (1 mile). However, the vegetation and terrain descriptions in the notebooks were of sufficient detail and taxonomic accuracy that in most cases we were able to narrow the collecting site down to within a few hundred metres. Often, for instance, we were able to base the location on the particular tree species observed in the notebook – in a number of cases we suspect that the trees were sufficiently old to be the same ones referred to in the notebook. Much of our collecting was in cleared land, where small patches of roadside vegetation were present. The clearing of native habitat in our survey area occurred mostly before 1921 with approximately 44% of NSW cleared, especially by ringbarking (Glanznig 1995), and little land has been returned to its natural state. Thus, the general pattern of vegetation in the area was likely very similar to the time of the 1940s surveys. The full collection of field notebooks archived in the ANIC includes an extremely wide range of habitats, some being relatively homogeneous in vegetation structure (e.g., the Nullarbor plain), and thus relocation confidence would not always be as high as in our particular case.

Resurvey Limitations

A number of potential issues may limit the comparability of our survey results with those of Key and Chinnick, as described in detail in the methods. Environmental conditions are an issue in terms of short-term activity and long-term population growth, and possibly also migration/emigration in the case of nomadic species, such as the Australian plague locust, *Chortoicetes terminifera*.

In the short term, temperature has a strong influence on grasshopper detectability; in cold weather, grasshopper detectability may decline strongly due to lack of flying or hopping whereas in warm weather capture success may decline due to enhanced escape behaviour. Overall, our measurements of potential ('operative') grasshopper temperature were consistently higher than the 1940s survey (Fig. 6a-d), which may have increased our detection rates. However, inferred maximum operative temperatures were always above 30 °C during both survey periods (Fig. 6d), so it appears that all days were suitable for grasshopper detection across both surveys. In the 1940s, the early morning/late afternoon collections may have more often been suboptimal for detection than in our 2019 survey.

An additional issue is misidentification – comprehensive keys for the Australian Orthoptera are not available and many species are yet to be described, despite having temporary genus and species numbers (Rentz et al. 2003). Moreover, we collected many species in their nymphal stages (Table 2), and grasshopper nymphs are often highly variable and lack diagnostic features, rendering them difficult to identify to the species level. For some genera, the differences among the species were too subtle to confidently identify to the species level in the field (e.g. *Austroicetes*). For others, species identification required dissection of male phallic structures, which was challenging in the field setting (e.g. *Praxibulus*). Morphological convergence is quite rampant in the Australian grasshoppers, and some genera look externally very similar. For example, Key and Chinnick found *Azelota* at four sites but we never found this genus; Rentz *et al.* (2003) note that this species may be confused with *Peakesia* (which we found in many more sites than in the historical surveys) and we concede the possibility of a small number of taxonomic errors in our data. Nevertheless, we are highly confident of our genus-level identifications overall and, in several cases, the genera are monotypic, making it easy to ascertain the identification. Besides the aforementioned exceptions, we are confident that we correctly identified all other species.

Comparisons of Grasshopper Richness and Success

Overall, we found more species over more sites than were found in the 1940s surveys, except for sites in the far north of our study, between Nyngan and Bourke (Fig. 2). During our survey, inland NSW was in the grip of an intense drought and, although rain had recently fallen around Bourke, it was too recent to have stimulated grasshopper population growth (visually, this area was extremely barren relative to other sites we visited). Indeed, there was a strong overall correlation of grasshopper abundance and, to a lesser extent, species richness, with rainfall and other moisture indices summed over a year for the 30 days prior to our survey dates (Figs 4, 7, 8). The 30-day offset gave the strongest association compared to using offsets of three weeks more or less (analyses not show) and, even though the soil moisture-derived metrics showed slightly stronger associations with abundance and richness than raw rainfall values, they were not substantially better. The absence of a relationship between rainfall-based metrics and the 1940s species richness may be due to the lower quality of the rainfall data from that time period.

The conditions in the year prior to the 1940s surveys were much wetter (Fig. 6e,f) than prior to the 2019 survey, but some species such as *Phaulacridium vittatum* and potentially *Acrida conica* do best in years of intermediate rainfall (David Hunter, pers. comm.), which may partially explain the higher species richness we observed. However, some species and genera were clearly less frequent in 1940s surveys compared to 2019 re-survey, with differences so large they transcend the limitations of comparing the surveys quantitatively (Fig. 3). The most striking were *Acrida conica* and *Macrotona* species, which were found in only a handful of locations in the 1940s but were widespread and abundant across our southern sites in the 2019 survey (Fig. 3). The differences between surveys in these two taxa may be due to interannual changes in abundance or range expansion due to systematic changes in habitat and climatic suitability. As discussed in the next section, an increase in grassy weeds (both species are grass-feeders) may have driven these changes but a more definitive answer must await further notebook transcription and resurveys.

Habitat Changes

The vegetation comparison revealed that many sites had undergone transitions of two major types: increased weedy grasses (mainly in the south east) and shrub thickening (mainly in the northern and inland areas; Fig. 1b). Both types of change are consistent with the literature, suggesting the ability of the notebooks to provide data that reliably reflect long-term vegetation trends. For example, the encroachment and thickening of woody species, particularly White Cypress Pine *Callitris glaucophylla*, has been described in inland New South Wales since the 1940s (Whipp *et al.* 2012), although the locations, periods and magnitude of change are variable and much-debated (Witt *et al.* 2010, p.200). Similarly, there is little doubt that invasive grasses have increased in richness, cover and distribution across inland Australia, although only a few studies have drawn on long term data to directly demonstrate this (Clarke *et al.* 2005). Many of these broad-scale changes in vegetation are known to be linked to large-scale changes in land-use (Lunt and Spooner 2005; Lunt *et al.* 2006).

Such qualitative shifts in vegetation composition are often summarised by state-and-transition models (Westoby *et al.* 1989; Spooner and Allcock 2006). These models represent different expressions of vegetation within a system, for example, a shrubby verses a grassy formation, which may transition from one to another by land use, for example, grazing or timber cutting. Given that many grasshoppers show a preference for certain food plants (e.g., grasses, daisies or shrubs) (Chapman and Sword 1997), and certain vegetation structures for thermoregulation and reproduction (e.g., bare ground or shrubs), we should expect the grasshopper fauna to be closely correlated with the predominant vegetation state. If indeed Key's notebooks can help identify states and transitions, as our survey suggests, this may provide a fruitful way to analyse shifts in the grasshopper fauna in relation to shifts in the ecosystem, both in land use and vegetation structure.

Evaluating what these shifts may mean is more challenging. It is important to note that substantial vegetation change had already occurred in the period between agricultural colonisation (1830s) and the 1940s (Lunt *et al.* 2006), and that the pollen record confirms that vegetation patterns in inland Australia were not static under pre-colonial aboriginal management (e.g. Luly 2001 for Callitris pine changes in the Pleistocene). So, while the 1940s surveys represent a baseline for comparison, they do not represent a pristine state nor a static archetype.

Conclusion and Future Prospects

Our study indicates that there is great potential for using Key's field notebooks to establish a strong basis for changes in the orthopteran fauna of Australia since the early-mid 20th century, as well as the nature and timing of habitat change. Even with our relatively small-scale effort (45 sites over six days) we were able to infer substantial range or abundance shifts in some taxa as well as tentative evidence of a general change of state in the vegetation. The strong connection, and rapid responses, of grasshoppers to vegetation change, and their generally conspicuous and abundant nature, makes them particularly valuable as general bioindicators of environmental change (Nufio *et al.*, 2010).

Our analysis gave no evidence of decline in the grasshopper fauna, but further analysis of the remaining data in Key's field notebooks would provide a more definitive perspective. The trend towards collapse in insect populations is likely driven by one of four major drivers of species extinction, namely, habitat modification, pollution (pesticides and fertilizers), the spread of introduced predators and pathogens, and climate change (Potts *et al.* 2010; Dirzo *et al.* 2014; Sánchez-Bayo and Wyckhuys 2019; Wagner 2020). Despite these likely suspects, the mechanistic basis of these widespread declines remains unclear and the magnitude of invertebrate declines in Australia are poorly understood (Braby 2019). The detailed information on habitat change that can be gleaned from Key's notebooks may help with the interpretation of any detected cases of grasshopper decline, or indeed any other insect group found in similar habitats. For instance, the large-scale replacement of perennial native grasslands and shrublands with exotic species has been argued to favour some grasshopper species such as *Austroicetes cruciata* (Andrewartha 1943) and the notebooks may provide further evidence of this.

Future surveys could be undertaken a variety of ways. They may simply involve haphazard resurveys across all notebooks at matching times of year as opportunity arises, by multiple participants under a common set of survey protocols. Such a model may be amenable to citizen science efforts. Or, at the other extreme, they may be done as a concerted effort by the same participants in a more intensive manner to reduce surveyor bias and misidentification (Morrison, 2016; Shea, Peterson, Wisniewski, &

Johnson, 2011). Another, more hypothetico-deductive approach would be to determine sampling locations which are geographically alike (in terms of soil, climate, etc.), but differ in current vegetation and land management, then use these paired sites to test hypotheses that grasshopper communities have diverged due to land use and vegetation changes. This would allow formal assessments of the extent to which any changes represent community shifts verses faunal collapse. Overall, extended resurvey and comparison of Key's field notebooks will enable a more definitive picture of how grasshopper diversity has changed over the past century.

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SUPPORTING INFORMATION

Figure S1. Relative proportions of different vegetation types, as well as grass greenness, per site based on Table S1.

Table S1. The percentage cover of relevant vegetation and other habitat elements to grasshopper ecology as qualitative estimate across visited sites.

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Table 1. Summary of the site locations and survey dates, including assessments our confidence in the relocation, the degree of habitat change inferred, the number of species found for each survey period and a rank-order estimate of overall abundance for the 2019 survey.

Note-book	Odo-meter	Coordinates	Survey Date	Resurvey Date	Relocation Confidence	Site Change	Species 1940s	Species 2019	Abundance 2019
16	11533	E148°40.529 S34°24.991	28/10/1946	21/11/2019	certain	minor	6	1	1.5
16	11615	E147°25.961 S34°26.163	29/10/1946	22/11/2019	high	negligible	3	6	1
16	11626	E147°14.803 S34°24.068	29/10/1946	22/11/2019	low	negligible	2	2	2
16	11635	E147°07.978 S34°30.928	29/10/1946	22/11/2019	high	minor	5	3	1.5
16	11644	E147°01.825 S34°20.291	29/10/1946	22/11/2019	certain	minor	4	6	1.5
16	11655	E146°51.008 S34°21.030	29/10/1946	22/11/2019	certain	minor	8	5	2
16	11664	E146°42.567 S34°18.319	29/10/1946	22/11/2019	certain	negligible	8	2	2
16	11676	E146°30.168 S34°15.977	29/10/1946	22/11/2019	medium	major	7	1	2
16	11685	E146°21.595 S34°13.846	29/10/1946	22/11/2019	high	negligible	8	1	1
16	11724	E145°57.331 S34°11.784	29/10/1946	23/11/2019	medium	major	7	1	2
16	11737	E145°49.149 S34°04.663	29/10/1946	23/11/2019	high	major	9	1	2
16	11752	E145°39.279 S33°54.619	29/10/1946	23/11/2019	high	major	5	0	1
16	11765	E145°35.254 S33°43.273	29/10/1946	23/11/2019	high	minor	4	0	1
16	11785	E145°30.798 S33°28.168	29/10/1946	23/11/2019	certain	negligible	2	3	1
20	14851	E149°18.495 S35°21.693	29/11/1948	19/11/2019	certain	negligible	8	4	2
20	14907	E149°45.960 S35°18.343	29/11/1948	19/11/2019	certain	negligible	6	8	3
20	14926	E149°49.050 S35°06.302	29/11/1948	19/11/2019	certain	minor	9	2	2
20	14942	E149°45.185 S34°56.832	29/11/1948	19/11/2019	high	negligible	10	2	3
20	14959	E149°42.395 S34°44.097	30/11/1948	20/11/2019	medium	major	3	5	2
20	14967	E149°38.212 S34°38.746	30/11/1948	20/11/2019	high	minor	4	2	2
20	14978	E149°33.390 S34°31.270	30/11/1948	20/11/2019	high	minor	5	3	1
20	14987	E149°26.144 S34°27.034	30/11/1948	20/11/2019	high	minor	6	2	2

20	14996	E149°17.780 S34°27.698	30/11/1948	20/11/2019	high	negligible	5	3	2
20	15005	E149°10.147 S34°26.253	30/11/1948	20/11/2019	medium	major	5	3	2
20	15015	E149°03.225 S34°23.629	30/11/1948	20/11/2019	certain	negligible	6	2	2.5
20	15022	E148°56.737 S34°23.082	30/11/1948	20/11/2019	high	minor	4	2	3.5
20	15032	E148°48.675 S34°23.011	30/11/1948	20/11/2019	high	major	8	6	1
20	15050	E148°35.811 S34°22.682	1/12/1948	21/11/2019	high	major	8	5	1.5
20	15061	E148°27.466 S34°19.525	1/12/1948	21/11/2019	certain	minor	7	2	2
20	15066	E148°22.385 S34°18.512	1/12/1948	21/11/2019	high	minor	9	2	2
20	15078	E148°15.451 S34°15.034	1/12/1948	21/11/2019	certain	minor	5	1	2
20	15086	E148°15.958 S34°08.337	1/12/1948	21/11/2019	certain	minor	6	7	1
20	15094	E148°13.454 S34°01.423	1/12/1948	21/11/2019	high	negligible	6	1	1
20	15101	E148°09.591 S33°55.825	1/12/1948	21/11/2019	high	negligible	8	1	1
20	15109	E148°12.492 S33°54.352	1/12/1948	21/11/2019	high	negligible	5	6	1
20	15115	E148°18.430 S33°54.618	1/12/1948	21/11/2019	certain	negligible	6	2	1.5
20	15125	E148°27.163 S33°54.475	1/12/1948	21/11/2019	certain	negligible	6	6	2
20	15136	E148°36.747 S33°49.931	1/12/1948	21/11/2019	certain	minor	6	5	2
22	7536	E147°08.590 S31°31.512	21/10/1949	24/11/2019	high	minor	5	9	1
22	7546	E147°02.461 S31°24.468	21/10/1949	24/11/2019	high	minor	3	4	1
22	7556	E146°56.485 S31°17.566	21/10/1949	24/11/2019	high	minor	3	4	1
22	7566	E146°50.291 S31°10.372	21/10/1949	24/11/2019	high	minor	2	7	1
22	7576	E146°44.299 S31°03.395	21/10/1949	24/11/2019	high	minor	2	1	1
22	7586	E146°38.350 S30°56.413	21/10/1949	24/11/2019	high	minor	1	1	1
22	7596	E146°32.592 S30°49.495	21/10/1949	24/11/2019	low	negligible	1	8	1

Table 2. Summary of total number of sites each species and genera, including their life stages, recorded during 1940s and 2019 re-survey.

Family	Genus	Species	Sites 1940s	Sites 2019	Stage 1940s	Stage 2019	Per Genus 1940s | 2019
Acrididae	*Acrida*	*conica*	1	19	j	a+j	1|19
Acrididae	*Aiolopus*	*thalassinus*	1	1	a	j	1|1
Acrididae	*Austroicetes*	sp.		10		a+j	46|10
Acrididae	*Austroicetes*	*arida*	1		a		
Acrididae	*Austroicetes*	*cruciata*	22		a		
Acrididae	*Austroicetes*	*frater*	9	4	a+j	a	
Acrididae	*Austroicetes*	*interioris*	6		a		
Acrididae	*Austroicetes*	*pusilla*	3	1	a	a	
Acrididae	*Austroicetes*	*vulgaris*	5		a+j		
Acrididae	*Azelota*	sp.	4		a		4|0
Acrididae	*Brachyexarna*	*lobipennis*	12	5	a	a+j	12|5
Morabidae	*Capsigera*	sp.		4		j	0|4
Acrididae	*Chortoicetes*	*terminifera*	15	10	a+j	a+j	15|10
Acrididae	*Coryphistes*	sp.	1		a		1|7
Acrididae	*Coryphistes*	*ruricola*		7		a+j	
Acrididae	*Cryptobothrus*	*chrysophorus*	4	4	a	a	4|4
Acrididae	*Ecphantus*	*quadrilobus*	2	3	a+j	j	2|3
Acrididae	*Eumecistes*	*gratiosus*		1		j	0|1
Acrididae	*Froggattina*	*australis*		1		a	0|1
Acrididae	*Gastrimargus*	*musicus*	1	6	j	a+j	1|6
Acrididae	Genus novum *5(?)*	sp.	2		a		2|0
Acrididae	Genus novum *7(?)*	sp.	1		a		1|0
Acrididae	Genus novum *16*	sp.	1		a		1|0
Acrididae	Genus novum *22*	sp. 1	2		a		2|0
Acrididae	Genus novum *28*	sp.		2		j	0|2
Acrididae	Genus novum *48*	sp.	1		a		1|0
Acrididae	Genus novum *95*	*ochracea*		1		a	0|1
Acrididae	Genus novum *115*	sp.		1		a	0|1
Acrididae	*Goniaea*	sp.	5	2	a	a+j	7|34
Acrididae	*Goniaea*	*australasiae*	2	11	a	a+j	
Acrididae	*Goniaea*	*carinata*		1		a	
Acrididae	*Goniaea*	*opomaloides*		17		a+j	
Acrididae	*Goniaea*	*vocans*		3		a	
Acrididae	*Histrioacrida*	*roseipennis*		1		j	0|1
Morabidae	*Keyacris*	*marcida*	1		a		1|1
Morabidae	*Keyacris*	*scurra*		1		a	
Acrididae	*Laxabilla*	*smaragdina*		1		j	0|1
Acrididae	*Macrolopholia*	sp.	1		a		1|0

Acrididae	*Macrotona*	sp.	1	24	j	j	3|27
Acrididae	*Macrotona*	*australis*	1		a		
Acrididae	*Macrotona*	*securiformis*		3		a+j	
Acrididae	*Micreola*	sp.		1		a+j	0|1
Acrididae	*Oedaleus*	*australis*	6	23	a+j	a+j	6|23
Acrididae	*Peakesia*	sp.		5		j	6|8
Acrididae	*Peakesia*	*hospita*	6	3	a	a+j	
Acrididae	*Perbellia*	sp.		1		j	0|1
Acrididae	*Perelytrana*	sp.		1		j	0|1
Acrididae	*Pespulia*	sp.		2		a+j	0|2
Acrididae	*Phaulacridium*	*vittatum*	5	23	a+j	a+j	5|23
Acrididae	*Praxibulus*	sp.	7	19	a+j	a+j	9|23
Acrididae	*Praxibulus*	sp. *1*		2		a+j	
Acrididae	*Praxibulus*	sp. *2*		2		a+j	
Acrididae	*Praxibulus*	*duplex*	1		a		
Acrididae	*Praxibulus*	*insolens*	1		j		
Acrididae	*Pycnostictus*	sp.	6		a+j		13|12
Acrididae	*Pycnostictus*	sp. *1*		1		a	
Acrididae	*Pycnostictus*	*seriatus*	7	11	a	a+j	
Acrididae	*Qualetta*	*maculata*	3	2	a+j	a+j	3|2
Acrididae	*Schizobothrus*	*flavovittatus*	1		a		1|0
Acrididae	*Stropis*	*maculosa*		1		j	0|1
Acrididae	*Tapesta*	sp.	1		a		1|0
Acrididae	*Urnisa*	sp.	1		a		3|1
Acrididae	*Urnisa*	*guttulosa*	2	1	a	j	

Figure Captions

Figure 1. (a) Survey locations in comparison to mean total annual rainfall (bioclim variable 12), and (b) sites where significant habitat change was inferred. In (b), brown squares indicate sites where habitat is inferred to have become shrubbier; green squares indicate sites inferred to have become weedier and more grass-dominated (size proportional to magnitude of change).

Figure 2. Species richness for: (a) the 1940s surveys of Key and Chinnick, and (b) our 2019 resurvey. The size of the black points indicates the magnitude of species richness.

Figure 3. Occurrences of the more common genera in the two collecting periods, with mean annual rainfall plotted in the background (see Fig. 1 for rainfall scale).

Figure 4. (a) Abundance scores for the 2019 surveys, and (b) rainfall cumulated for 1 year starting 30 days prior to the surveys.

Figure 5. Observed and predicted: (a) air temperature at 1.2 m, (b) ground temperature in sun, (c) ground temperature in shade, and (d) operative (i.e. potential) body temperature in the sun. Correlation coefficients (*r*) are indicated on the plots as well as the 1:1 line. All *P*-values for correlations were < 0.01 except for air temperature (*P* = 0.146).

Figure 6. Estimates of environmental conditions during the 1940s surveys compared to the 2019 resurvey for: (a) air temperature at 1.2 m, (b) unshaded ground temperature, (c) shaded ground temperature, (d) operative (potential body) temperature, (e) rainfall, and (f) a plant growth growing

degree days index, the latter two being based on a 12-month period extending backwards from 30 days prior to sampling. Each point represents a site.

Figure 7. Semi-quantitative assessments of grasshopper site abundance during 0.5 hr surveys plotted against: (a) total rainfall, (b), summation of soil moisture-based estimate of plant moisture content, (c) summation of soil moisture-based plant presence index, and (d) an estimate of plant growth based on growing degree days when soil moisture was above the permanent wilting point. Environmental conditions are based on a 12-month period extending backwards from 30 days prior to sampling. The Spearman's rank correlation, 'rho', is indicated for each plot. The abundance scores are described in Methods. Each point represents a site.

Figure 8. Species richness during 0.5 h surveys for the 1940s (a, b) and 2019 (c, d) plotted against total rainfall (a, c) and an estimate of plant growth based on growing degree days when soil moisture was above the permanent wilting point (b, d). Environmental conditions are based on a 12-month period extending backwards from 30 days prior to sampling. The Spearman's rank correlation, 'rho', is indicated for each plot. Each point represents a site.

Table S1. The percentage cover of relevant vegetation and other habitat elements to grasshopper ecology as qualitative estimate across visited sites.

Site No.	Eucalyptus	Acacia	Casuarina	Callitris	Shrub	Chenopod	Native herbaceous daisies	Weedy herbaceous daisies	Other forbs	Sedge	Native grass	Exotic grass	Bare	Litter	Grass greenness
20_14851	10	8	0	0	10	0	2	0	1	0	30	0	10	60	0
20_14907	10	5	0	0	10	0	0	0	0.1	1	20	5	50	10	0
20_14926	10	0.1	0.1	0	5	0	0.1	0	0.9	0	2	0	40	45	0
20_14942	1	0	0	0	5	0	2	0	0	0	70	5	20	5	0
20_14959	0	0	0	0	3	0	0.1	0	4.9	0	30	60	1	40	0
20_14967	15	0.1	0	0	1	0	0.1	0	0	0	50	40	5	40	0
20_14978	0	10	0	0	10	0	0	5	5	0	25	60	1	30	100
20_14987	25	1	0	0	4	0	0	1	2	0	0	85	5	20	100
20_14996	15	1	0	0	5	0	0	1	1	0	70	1	15	15	50
20_15005	3	0	0	0	1	0	0	0	0.1	1	1	20	30	30	0
20_15015	1	3	0	0	5	0	0	0	0.1	1	80	2	2	40	0
20_15022	30	3	0	0	5	0	0	0	0.1	0.1	35	5	20	40	50
20_15032	5	0.1	0	0	0.1	0	0	0.1	0.1	0	2	38	20	40	0
16_11533	20	0	0	0	0.1	0	0	0	1	5	0.1	40	10	50	50
20_15050	25	2	0	0	3	0	0.1	0	0.9	0.1	1	45	5	60	50
20_15061	20	0	0	0	0	0	0	0.1	0	0.1	1	40	5	60	0

20_15066	25	0	0	0	0	0	0	0	1.1	1	1	40	5	60	50
20_15078	15	0.1	0.1	0	0.1	0	0	0	0.1	0	1	50	20	50	0
20_15086	5	0	0	0	1	0	0	5	0	0	0	65	5	30	0
20_15094	15	0	0	0	2	0	0.1	0	0	1	20	0	5	70	0
20_15101	20	3	1	0	5	0	0	0	0.1	0	10	0	5	85	0
20_15109	20	0	0	0	10	0	1	0	0	0	5	0	15	70	0
20_15115	10	2	0	0.1	20	0	0.1	0	0	0	5	1	40	50	0
20_15125	20	1	0	0.1	22	0	0.1	0	0	0	3	2	45	50	0
20_15136	25	0	0	0.1	0	0	0	0	3	30	7	3	2	70	0
16_11615	25	5	0	10	5	0	0.1	0	0	0	1	0	40	60	0
16_11626	15	5	0	3	5	0	0.1	0	0	0	1	1	20	75	0
16_11635	20	1	0	0.1	10	0	0.1	0	0.9	0	2	0.1	5	80	50
16_11644	2	0	0	30	0	0.1	1	0	0.9	0	25	1	55	20	0
16_11655	5	0.1	0	30	0	0	0.1	0	0.9	0	5	5	50	40	0
16_11664	20	3	0	5	4	0	0	0	0.1	0	35	0	30	35	50
16_11676	0	2	0.1	10	35	0.1	3	0	1.9	0	25	0	20	45	50
16_11685	2	5	0.1	10	45	1	0	0	1	0	10	10	60	20	50
16_11785	0.1	0.1	0	0	5	3	2	0	0	0	0.5	0.5	55	40	0
16_11765	0	0	0.1	50	3	0.1	1	0	0.9	0	0.1	0	30	65	0
16_11752	5	10	1	1	5	5	1	0	0	0	15	5	40	30	50
16_11737	3	5	5	1	25	10	1	0	0	0	15	2	40	30	50
16_11724	0.1	5	0	0	20	5	1	0	0	0	10	15	45	20	50
22_7536	5	1	0	1	2	3	0	0	0	0	10	0.1	65	20	50

22_7546	3	10	0	0	10	3	0.1	0	1.9	0	2	0.1	70	10	50
22_7556	10	2	0	3	15	0.1	0	0	0.9	0	3	0	70	20	0
22_7566	5	2	0	2	15	0	0	0	0.1	0	0.1	0	70	25	0
22_7576	15	1	0	5	15	0.1	0	0	0	0	0.1	0	50	45	0
22_7586	5	0.1	0.1	2	15	0.1	0.1	0	0	0	1	0	80	15	50
22_7595	5	1	0	0	15	0.1	0.1	0	1.8	0	1	0	75	20	50

Figure S1. Relative proportions of different vegetation types, as well as grass greenness, per site based on Table S1.