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学位授与の日付	平成１８年９月３０日
論　文　名	「A study on species and behavioral diversity of hilltopping butterflies on hilltops in Japan （日本の山嶺における山頂占有性チョウ類の種と行動の多様性に関する研究）」
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論文要旨

Hilltops are essential landscape elements for life cycle completion of many insect taxa belonging to diverse orders, including butterflies, all over the world. Species, rare or even common but whose receptive females are widely dispersed in space and time aggregate on them for mating. There have been studies on hilltopping exclusively focused on behavioural ecology aspects on one site and a few or only one species at a time. However, conservation aspects and their possible generalization to other hills, other taxa, other countries were never investigated. The objective of the present study is: to clarify species and behavioural diversity of hilltopping butterflies on hilltops in Japan;　investigation of how far their phenology and distributional patterns on hilltops are different from species to species and hilltop to hilltop for the same species; determination of the hilltop kinds which are hilltoppers hotspots and should be prioritised for conservation of butterflies or other insects biodiversity.

Chapter 1. Faunal and phenological diversity of hilltopping butterflies on two mountains

It is needed to clarify if hilltopping is a standardized phenomenon with only one purpose and to find a way to discriminate (non)hilltoppers　in the field. By using the

frequency of visits in 5-m radius circles scattered on summit, subsummit and slope on the hill, annual surveys were conducted in Mts Katsuragi and Nijo, surrounded by urbanized areas. Mt Katsuragi (960 m alt.), has a bare and grassy hilltop and deeply forested slopes. Mt Nijo, with two peaks, Medake and Odake (474 and 517 m alt.), has lightly forested hilltops and slopes. A resource use definition of hilltopping based on a criterium comparing the sum of visit percentages in " broad summit " (summit and subsummit) circles with that obtained when the species would be randomly distributed on the hill, enabled a separation of (non)hilltoppers in the total list of observed species.

A total of 55 species were observed, with 53 species seen in Mt Katsuragi, 42 in Medake and 31 in Odake. Twenty nine species were shared by the 3 peaks. Fifteen species out of 55 could be discriminated as hilltoppers, with some of them hilltopping on only one mountain or hilltop though they were present on both sites. Five hilltopper species were common to the 3 peaks while 11, 10, and 7 species were hilltopper on Mt Katsuragi, Medake and Odake, respectively. Though some species were very abundant on the summit in the 3 seasons or in only 2 or 1 season(s), variability in relative abundance and dominance ranking status existed between peaks for those 15 hilltoppers.

Chapter 2. Behavioral diversity of hilltopping butterflies on two mountains

By comparing male behavioural patterns of the hilltopping species from both mountains on summit, subsummit and slope, hilltoppers could be classified into 5 types of hilltopping (Types A1, A2, B, C1 and C2) with different or combination of several purpose(s). Some species had a higher percentage of fighting on summit than on subsummit and slope (Type A). Others had foraging as dominant behaviour on both summit and subsummit though fighting was also present and somewhat more abundant on the subsummit (B). At last, others were hilltopping in sufficient numbers only in summer and on peaks of relatively high altitude (C). Type A species could be subdivided into 2: some perching proportion always existed on summit and subsummit (A1) or never perching on any zone and with a relatively high percentage of visits on slope (A2). Similarly, Type C species were segregated into 2: flying as dominant behaviour, with fighting in equal proportion on the summit and subsummit (C1) or courtship in a non negligible proportion on both summit and subsummit with relatively high percentage of foraging and fighting on both zones, though often higher on subsummit (C2).

Type A has mating as unique purpose, since fighting, among all behaviours compared, is the one with the strongest mating connotation. Type B species are exclusively migrant and combine 3 purposes: nectaring, mating and short stop on

hilltops during their migrations. In Type C, hilltops are used as temporal habitat during aestivation but, in Type C2, other purposes are also associated, such as breeding on foodplant, nectaring and mating. Behavioral patterns were consistent between both mountains for the same species.

Chapter 3. Movement patterns of dominant hilltoppers

In order to (dis)prove in Type A species the deliberate character of hilltopping and to determine whether those hilltoppers commute with the mountain foot and their level of fidelity to a particular hilltop, 3 types of mark-release-recapture experiments (Experiments 1-3) were carried out. In Exs 1, 2 and 3, specimens were, respectively, captured on the summit and released at the mountain foot, captured and directly released on the summit, captured on the summit and released in the saddle between the two peaks. Dominant species showing a hilltopping distribution in both mountains were surveyed: *P. machaon* (*Pm*) and *A. hyperbius* (*Ah*).

In Ex. 1, both species were proved to be real hilltoppers (deliberate flight to the hilltop) and almost same rates of recaptures were found for them, with more than 50% of individuals recaptured within one day after release. There was a tendency to come back more to one peak in both species, showing some insistence for it or a tendency of going up to the nearest peak. Both species came back more to the summit of one mountain, which may be due to some impact of altitude on the commuting rate. Besides, in one mountain, there was a tendency, though non significant, of hilltopping more in summer than in autumn for *Ah*.

In Ex. 2, recapture rates were similar to Ex. 1 for both species, which supports the commuting hypothesis. In Ex. 2 and 3, more “returns” to the same peak as original marking than exchanges with the other peak occurred for *Ah* but not *Pm*, which highlights some preference or insistence for a particular peak only in *Ah*.

The results demonstrate that both species showed similarity in their non random flight to the hilltop and commuting tendency in both mountains but differed concerning their degree of faithfulness to a certain peak. *Pm* seems thus to have a more open population type than *Ah*.

Chapter 4. Factors influencing microdistributions of hilltoppers on the summit

In order to elucidate the relative importance of climatic factors on hilltop microdistributions, horizontal distributions of 4 dominant species on the hilltop were analysed. By controlling for time of day, circle positions, and other weather parameters, the number of (non) visit events for particular categories of wind speed or light

intensity were compared. Only in the case of *Ah*, some impact occurred: this species avoided moderate and strong wind speeds and low and moderate light levels.

Vertical distribution of *Pm* was also analysed and the results showed that there is a tradeoff between maximum visual range related to the vegetation structure of particular peak and some weather factors.

In order to determine the level of convergence of species microdistributions on the hilltop among peaks, the same observation method as in Ch.1 was used. By using rank correlations, group or only isolated convergences were found, according to the peak. Though some species associations were similar between certain peaks, they differed on others, which highlights a diversity of hilltoppers responses to varying hilltop environment.

For determining the minimal topographical and/or vegetational cues for hilltoppers, two kinds of analyses were performed: rank order correlations of visits in summit circles with a series of best candidate environmental factors; 3 types of cluster analyses classifying summit circles of both mountains by their similarity of community structure, behavioural activities for 4 dominant hilltoppers, and environmental factors, respectively. A list of key factors were shown to influence summit microdistributions of hilltoppers. A same factor placed in a different mountain context lost its meaningfulness for some species but not for others.

Results of this study revealed the diversity of hilltopping phenomenon in butterflies on a spatial, temporal and behavioural point of view and the utmost importance of vegetation structure and topographical factors above climatic ones in determining the abundance and diversity of hilltoppers. From those findings, guidelines for conserving butterfly biodiversity on hilltops are proposed. Large, topographically complex hilltops, with a mosaic of micro-environments and still a high biodiversity on mountain foot and slopes, should be hotspots for hilltoppers and privileged in conservation.

審査結果の要旨

チョウ類を含む多くのグループに属する昆虫が生活史の中で山頂を利用する。一般にチョウ類では、個体数が少ないか、あるいは雌が広い範囲に散在する種が配偶の目的で山頂に集まり、雄はそこになわばりを形成する（山頂占有性）。しかし、これまでは特定の種の行動生態学的な側面のみが盛んに研究されてきたが、保全生態学的な側面あるいは異なる山、種、地域を比較する包括的な調査は行われてこなかった。そこで本研究は、日本の山嶺における山頂占有性チョウ類の種と行動の多様性を明らかにすること、

異なる山嶺におけるチョウ類各種の季節消長や分布パターンの違いを調査すること、山頂占有性チョウ類の多様性豊かな山嶺の特徴を解析し、チョウ類を含む昆虫類の生物多様性保全のために重要な要因を明らかにすることを目的として行われた。

第 1 章では、山頂占有性チョウ類を識別するとともに、その季節消長を明らかにするために、大阪・奈良府県境の（大和）葛城山（標高 960m）および二上山の２つのピーク（雄岳 517m、雌岳 474m）の山頂、亜山頂、斜面に半径５ｍの架空の円形調査地を多数設定し、一定の調査時間内に各観察円を訪れたチョウ類の種と個体数、行動を記録した。 その結果、葛城山から 53 種、雌岳から 42 種、雄岳から 31 種、合計 55 種のチョウ類が確認され、そのうち 29 種が３つのピークで共通に見られた。この調査においては、統計的に「広義の山頂」（山頂および亜山頂）に分布が偏っていた 14 種を山頂占有性種と判定した。このうち 5 種は３つのピークに共通していたが、10、10、7 種はそれぞれ、葛城山、雌岳、雄岳のみで山頂占有性を示した。たとえば、キアゲハなどは、春から秋まで山頂で見られたが、ウラナミシジミのように夏から秋のみに多い種もいた。

第 2 章では、上記 15 種類の山頂占有性種を対象に、雄の静止、飛翔、種内・種間闘争、採餌などの各行動の頻度を解析することにより、山頂占有種を５つのタイプに分類した。タイプ A1 は、山頂になわばりを形成し配偶場所として利用する狭義の山頂占有性種で、キアゲハやツマグロヒョウモンが該当した。ナミアゲハなども、同様に配偶の目的で山頂を利用するが、斜面を含む蝶道を形成し静止することがないのでタイプ A2 とした。山頂を吸蜜、配偶、移動中の着陸場所の３つの目的で利用するイチモンジセセリなどはタイプ B とした。タイプ C は山頂を夏季の一時的な生活場所として利用する種としたが、テングチョウなど（タイプ C1）では吸蜜や配偶、モンキチョウなど（タイプ C2）では寄主植物周辺での繁殖なども認められた。

第 3 章では、山頂占有性チョウ類の動態を明らかにするために、キアゲハとツマグロヒョウモンを対象に葛城山と二上山において３種類の標識再捕実験を行った。実験１では、山頂で捕獲した雄成虫を標識後山麓で放したが、両種とも一定の割合で山頂に戻ることが確認された。実験２では、山頂で捕獲した雄成虫を標識後山頂で放したが、山頂にとどまる時間は短く、翌日以降の再捕獲率は実験 1 と同程度であったことから、山頂と山麓との日々の往復の可能性が示された。実験３では、二上山の雌岳または雄岳の山頂で雄成虫を捕獲し、標識後２つのピークの間の尾根で放逐した。この実験では実験２と同様、両種とも元のピークでより多くの個体が再捕獲され、特定のピークに執着する性質が示された。

第 4 章では、山上における山頂占有性チョウ類の微小分布と気象要因との関係を主要４種について解析した。キアゲハの分布は風と無関係であったが、ツマグロヒョウモンは強風条件を避けた。両種とも高照度に選好性を示したのに対して、夕方近くに山頂に現れるアカタテハとヒメアカタテハは暗い条件を好んだ。また、キアゲハは雌岳では低木上に、高木の多い雄岳ではなわばりを樹冠に形成することが多かった。山上における

山頂占有性チョウ類の分布は、どの種についても一様ではなく、種ごとに異なっていたが、各種の場所の選好性には季節や年に関わらず一貫性が認められた。そこで、地形や植生などの要因と場所の選好性について解析したところ、裸地や草地、樹木、小道の交叉、ベンチなどの人工物、地面の起伏、見晴らしなどさまざまな要因あるいはそれらの組み合わせが各種のなわばり形成の場所の決定に関わっていることが明らかになった。

以上のように、本研究では山頂占有性チョウ類の山上における空間的、時間的、行動学的な多様性および植生構造や地形要因がそれらの種の個体数や多様性、微小分布を決める重要な要因であることを明らかにした。そして、これらの結果にもとづき、山頂占有性チョウ類の生物多様性を保全するための山上植生のあり方について検討を行った。これらは昆虫学や生態学などの基礎分野ばかりでなく、生物多様性保全に関わる応用分野にも寄与するところが大きい。よって最終試験の結果とあわせて、博士（学術）の学位を授与することを適当と認める。